Papers and Proceedings of

The Royal Society *of* Tasmania

Volume 151
December 2017

Papers and Proceedings of

The Royal Society *of* Tasmania

MUSEUMS VICTORIA
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Edited by M. Davies
and published by the Society

Volume 151
December, 2017

THE ROYAL SOCIETY OF TASMANIA
1843

Published by
The Royal Society of Tasmania
GPO Box 1166
Hobart, Tasmania, Australia 7000

www.rst.org.au

6 December 2017

ISSN 0080-4703

Cover illustration: A. Harold Masters & Alexander North: house in Elphin Road, Launceston, Tasmania.

Print Tasmania

PAPERS AND PROCEEDINGS OF THE ROYAL SOCIETY OF TASMANIA

VOLUME 151

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Publication of this volume was generously supported by the Government of Tasmania and the University of Tasmania.

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DISTURBANCE ECOLOGY OF TASMANIAN HIGHLAND GRASSLAND — AN OVERVIEW AND IMPLICATIONS FOR CONSERVATION MANAGEMENT

by Steven W. J. Leonard and Denna Kingdom

(with two text-figures, one plate and one appendix)

Leonard, S.W.J. & Kingdom, D. 2017 (6:xii): Disturbance ecology of Tasmanian highland grassland — an overview and implications for conservation management. *Papers and Proceedings of the Royal Society of Tasmania* 151: 1–10. ISSN 0080-4703. Department of Ecology, Environment and Evolution, La Trobe University, Bundoora, Victoria, 3086 Australia (SWJL*), Tasmanian Land Conservancy, Lower Sandy Bay, Tasmania, 7005 Australia (DK). *Author for correspondence. Email: s.leonard@latrobe.edu.au

Active manipulation of disturbances such as fire and grazing is often necessary to maintain or enhance biodiversity values in grasslands. However in many instances information is lacking on the disturbance regimes most likely to achieve conservation aims. This paper provides an overview of the effects of fire and grazing in Tasmanian highland grasslands, and the implications of these for conservation management of this vegetation. In Tasmania, highland grassland is defined as occurring above 600 m above sea level. The vegetation is typically dominated by species of *Poa*. Highland grassland is grazed by a suite of native herbivores and has a history of stock grazing, which continues at some sites of high biodiversity value. There is evidence that Indigenous Tasmanians regularly burnt highland grasslands and that Indigenous burning was instrumental in maintaining grassland at sites that otherwise would be forest. For highland grasslands below 1000 m asl, a reduction in the biomass of dominant grasses through disturbance is necessary in order to maintain plant species diversity. The use of periodic fire, together with native grazing, is likely to be beneficial in this regard. The combination of fire and grazing is also likely to prevent woody plant invasion and maintain vegetation structural heterogeneity. The near ubiquity of native grazing species means there is no ecological imperative for stock grazing. Low productivity of grasslands occurring above 1000 m means that competitive exclusion of interstitial species by grasses is unlikely and therefore active application of disturbance as a management tool will rarely, if ever be necessary. Disturbance management should be accompanied by a well-designed monitoring program and regular review of the management strategy.
Key Words: herbivory, fire regimes, alpine, sub-alpine, vegetation management, *Poa*, grasslands.

INTRODUCTION

Natural grasslands have been heavily transformed by human activity (Henwood 2010). Apart from conversion to introduced pastures, crops or urban settlements, a major factor in this transformation is alteration in disturbance regimes (Schnoor *et al.* 2015). Disturbance regimes are a critical determinant of grassland structure and composition (Belsky 1992, Tremont & McIntyre 1994, Leonard & Kirkpatrick 2004). Where grasslands are managed for conservation, active manipulation of disturbances such as fire and grazing is often necessary to maintain or enhance biodiversity values (Kirkpatrick *et al.* 2005). However, in many instances information is lacking on the disturbance regimes most likely to achieve conservation aims. A particularly contentious issue is the use of livestock grazing as a tool for achieving biodiversity conservation goals (Kirkpatrick *et al.* 2005, Lunt *et al.* 2007). While several studies have indicated that livestock grazing can promote biodiversity values (e.g., Gilfedder & Kirkpatrick 1994, Leonard *et al.* 2004), its effects are contingent on a range of factors such as vegetation composition, landscape context and site history (Lunt *et al.* 2007). Interactions of livestock grazing with other disturbances, in particular fire, also need to be considered (Fuhlendorf *et al.* 2008).

This paper addresses these issues in the context of highland grasslands in Tasmania, Australia. We define grassland as vegetation with <5% tree cover, and in which the tallest vegetation stratum with a cover of more than 10% is dominated by grasses or herbs. In Tasmania, highland grassland is defined as (usually) *Poa*-dominated grassland occurring above 600 m asl (the upper limit of *Themeda triandra* Forsk. in Tasmania), including grasslands occurring in the alpine (*sensu* Kirkpatrick 1983) zone (Kirkpatrick & Duncan 1987); see below for detailed description of the vegetation. These grasslands are also referred to as "montane grasslands" in some sources e.g., Bowman *et al.* (2013). This definition of highland grassland largely equates to that of the TASVEG community "Highland *Poa* grassland" (Kitchener & Harris 2013). While the focus of this paper is on grassland so defined, we recognise that highland grassland has floristic affinities and often co-occurs with grassy woodland, shrubland and sedgeland, and therefore some of the discussion may also be relevant to these communities.

There is currently approximately 26 000 ha of highland grassland in Tasmania (TVMMP 2013), comprising a significant proportion of remaining native grassland in temperate Australia (Balmer *et al.* 2004). No precise estimate is available as to what proportion of the pre-European invasion extent of highland grassland its current extent represents. However Kirkpatrick (1999) stated that about 60% of the pre-European extent of Tasmanian grassland overall remains, and that most of this occurs above 600 m. Highland grasslands in good condition have high biodiversity value, being floristically rich and often supporting threatened flora and fauna species (Kirkpatrick 1991). While 68% of highland grassland occurs within secure public and private reserves (DPIPWE 2016), some important examples are unreserved. Unreserved highland grasslands are subject to a range of threats, including outright loss through inundation or

conversion to exotic pasture or tree plantations. However even those within the reserve system may be reduced in extent or quality due to inappropriate disturbance regimes (e.g., Kirkpatrick & Balmer 1991, Bowman *et al.* 2013). Therefore understanding the effects of disturbance, and the disturbance regimes most conducive to maintaining biodiversity values, is crucial for effective conservation management of this vegetation.

We provide an overview of the effects of fire and grazing in Tasmanian highland grasslands, and their implications for conservation management. Our paper builds upon previous reviews that have included highland grassland in discussion of the ecology of Tasmanian grassy vegetation generally (Kirkpatrick *et al.* 1988, Kirkpatrick 1991, 1999). In addition to focusing specifically on the highland portion of Tasmanian grassland, we also synthesise more recent research with that included in previous reviews. While our paper does not take the form of a systematic literature review, we have endeavoured to be comprehensive in our inclusion of relevant literature (focusing on peer-reviewed journal papers), in particular that published since 1999 (when the last review of Tasmanian grassy vegetation was published; the results of a systematic review of this more recent literature are included in appendix 1).

VEGETATION DESCRIPTION AND ENVIRONMENTAL RELATIONSHIPS

Highland grasslands are typically dominated by one or more species of *Poa* (in particular *P. gunnii* Vickery and *P. labillardierei* Steud.), which may occur as a short or long (~10–100 cm) dense sward or as more isolated tussocks amidst forb-rich lawn (pl. 1). Heavily grazed areas may be dominated by *Rytidosperma nudiflorum* (P. Morris) Connor & Edgar. Grasslands in good condition exhibit a diverse array of forbs, with Asteraceae spp., *Velleia montana* Hook.f., *Ranunculus* spp., *Viola* spp. and *Geranium*

PLATE 1 — Examples of Tasmanian highland grasslands. A: long unburnt grassland exhibiting dense *Poa* tussocks and low abundance of interstitial species. B: Regularly burnt grassland. The area in the foreground has been burnt 1–2 years previously. Note space between *Poa* tussocks and abundance of forbs. The yellowish grassland patch in the left mid-ground has remained unburnt for longer.

spp. being common constituents. Emergent shrubs are also usually present, including *Epacris gunnii* Hook.f., *Acrothamnus hookeri* (Sond.) Quinn, *A. montanus* (R.Br.) Quinn, *Olearia algida* N.A. Wakef. and *Richea acerosa* (Lindl.) F.Muell. Scattered taller shrubs may also occur, such as *Hakea macrocarpa* R.Br., *Richea scoparia* Hook.f., *Coprosma nitida* Hook.f and *Tasmannia lanceolate* (Poir.) A.C.Sm. With increasing waterlogging, monocots such as *Empodisma minus* (Hook.f.) L.A.S.Johnson & D.F.Cutler, *Baloskion australe* (R.Br.) B.G.Briggs & L.A.S.Johnson and *Lepidosperma filiforme* Labill. become more prominent, and grassland grades into sedgeland or rushland. There is usually a sharp boundary between grasslands and adjoining forest or woodland (Fensham & Kirkpatrick 1992).

The most extensive areas of highland grassland occur on the Central Plateau, with outlying occurrences in the northwest and smaller, more isolated pockets in the northeast (Kirkpatrick 1999; fig. 1). These grasslands occur on relatively fertile, well-drained soils derived from dolerite, basalt, carbonate rocks and alluvium, although grassland on siltstone-derived soils occur in snow patches in the Cradle Mountain area and at the Walls of Jerusalem (Parry *et al* 2016). Kirkpatrick & Duncan (1987) identified six distinct highland grassland communities. The distribution of these communities was related to variation in soil fertility, summer temperature, drainage and precipitation. In addition, highland grasslands exhibit lower productivity at higher altitudes, due to lower temperatures and associated effects including frost heave, such that grasslands above ~1000 m asl take much longer to recover from disturbance than those below (i.e., decades cf. years; Gibson & Kirkpatrick 1989, Bridle *et al.* 2001, Kirkpatrick & Bridle 2013).

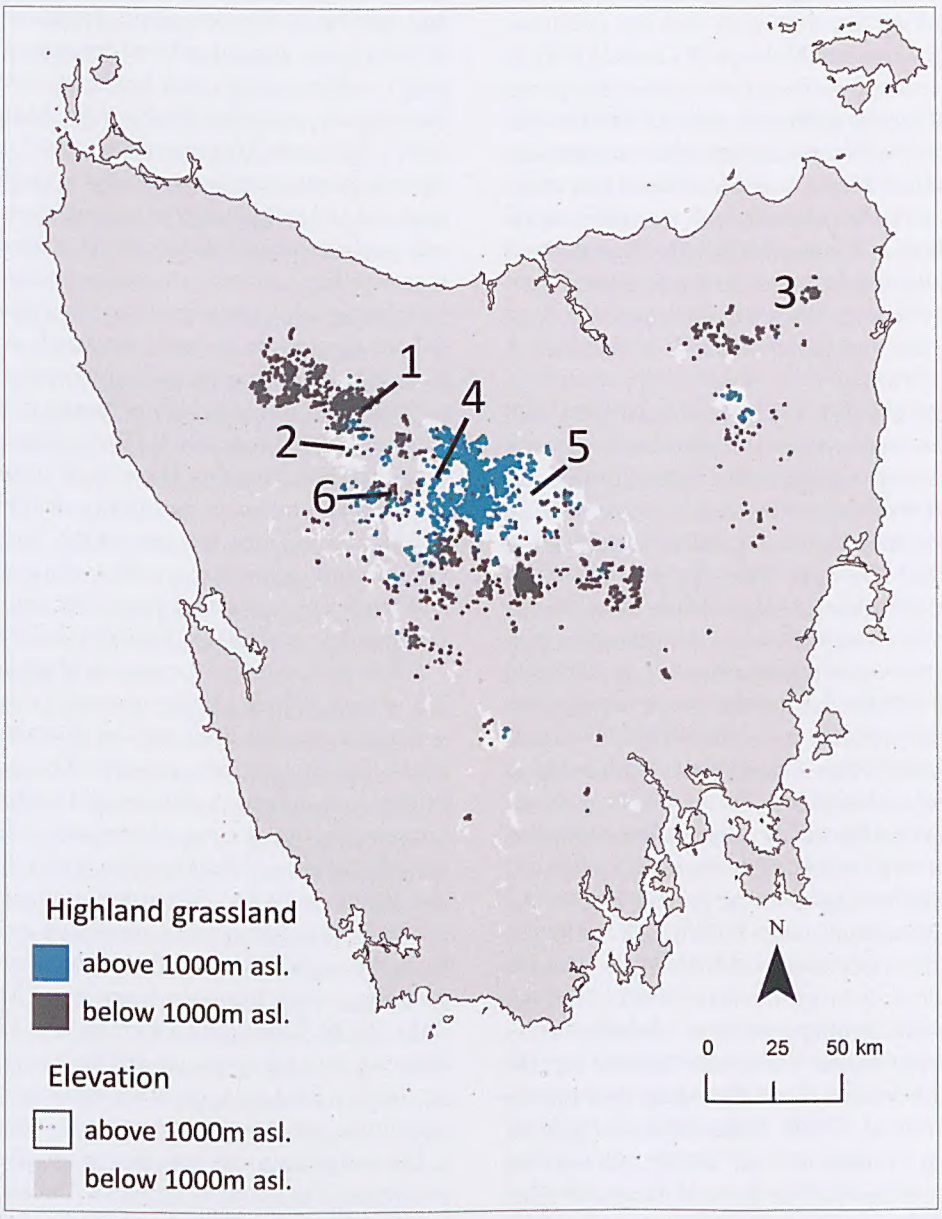

FIG. 1 — Distribution of highland grassland in Tasmania, and locations mentioned in text. 1 = Vale of Belvoir, 2 = Cradle Valley, 3 = Paradise Plains, 4 = Walls of Jerusalem, 5 = Central Plateau, 6 = Lee's Paddocks. Data sources: Land Tasmania (2007), TVMMP (2013).

DISTURBANCE ECOLOGY OF GRASSLANDS

General patterns

Grubb (1986) examined the mechanisms allowing the persistence of sparsely and patchily distributed species in English chalk grasslands. He proposed a model for this system in which most species remain relatively rare due to competition from the dominant perennial grasses, while defoliation of these grasses through disturbances such as fire and grazing produce niches in which less competitive species can persist. Grubb's model has been demonstrated to be widely applicable to grassland system dynamics. Grasslands subject to moderate disturbance exhibit higher species richness than those that are undisturbed (e.g., Stuwe & Parsons 1977, Fensham & Kirkpatrick 1989). However, where disturbance is frequent and/or intense, the resultant stress on plants may outweigh the benefits of reduced competition, resulting in a decline in both the dominant grasses and interstitial species (McIntyre & Lavorel 1994). In these circumstances weedy (often exotic) colonising species are promoted and species richness is reduced. The fact that grassland species richness is maximised at an intermediate point on a continuum between no disturbance and severe disturbance appears to be in accord with the intermediate disturbance hypothesis (Connell 1978). However the level of disturbance that promotes species richness is contingent on a number of factors, including productivity and evolutionary history, and therefore varies across systems (Milchunas *et al.* 1988).

Most natural grasslands are subject to grazing by wild and/or domestic animals. Many grasslands also experience periodic natural or anthropogenic fire. These disturbances are similar in that they remove vegetation biomass (Bond 2005) and therefore may promote species richness. For this reason conservation managers often apply one or other (or both) of these disturbances to grasslands. However fire and grazing differ in a number of ways, which means they may produce distinct vegetation outcomes (Lunt 1997a,b, Kirkpatrick *et al.* 2005). The key difference between fire and grazing as disturbances is in selectivity of biomass removed (Bond 2005). Fire is unselective, consuming all sufficiently dry vegetation that it encounters. In contrast, grazing animals will preferentially consume some elements of the vegetation over others. The degree of selectivity and the species selected vary amongst grazing species. For example, sheep preferentially target forbs (Leigh & Holgate 1978), while Eastern Grey Kangaroos (*Macropus giganteus* Shaw, 1790) feed mostly on grasses (Lunt 1991). For bulk feeders, such as cattle, feeding preference is based more on the vertical stature of plants, rather than species; i.e., the preference is for taller more accessible foliage over shorter plants (Noy-Meir *et al.* 1989). Other effects of grazers, such as trampling (Ferguson *et al.* 2010) and nutrient cycling and redistribution in the form of dung and urine (McNaughton 1984) can also be ecologically important.

A striking example of the potential for variation in the type of disturbance to shape grassy vegetation was provided by Lunt (1997a). In this study, the original grassy forest vegetation of the Gippsland Plain was found to have segregated under different disturbance regimes into grassland, associated with frequent burning and no grazing, and remnant grassy forest, which was lightly grazed by stock, with these "new" communities containing different subsets of the original flora. A major difference between these derived vegetation types was a preponderance of tall forbs in the burnt, ungrazed grassland remnants (Lunt 1997b). Similarly, different grazing species may also result in different outcomes in the vegetation. For example, Bridle & Kirkpatrick (1999) found that grassland on the Central Plateau subject to sheep grazing differed in structure and composition from that grazed by rabbits and Bennett's Wallabies (*Macropus rufogriseus* (Desmarest, 1817)).

The interactive effects of fire and grazing can be profound, as well as being difficult to predict by considering either disturbance in isolation (Fuhlendorf *et al.* 2010, Kirkpatrick *et al.* 2011). A well-known interaction of fire and grazing is the movement of grazers to regenerating recently burnt areas in order to consume nutritious "green pick", a phenomenon that has been widely exploited by hunters and pastoralists (Cubit 1996, Murphy & Bowman 2007). In South African savanna, the "magnet effect" of recently-burnt grassland was found to result in high grazing intensity and maintenance of grazing lawns when the burnt area was relatively small (Archibald & Bond 2004). When fires were large, grazing animals were more dispersed and therefore grazing intensity at any one point was reduced. Where grazers are strongly attracted to recently burnt areas the intense grazing and subsequent abandonment of patches can result in a shifting mosaic of vegetation states (Fuhlendorf & Engle 2004). The ecological heterogeneity brought about by this pattern of disturbance can be important in maintaining biodiversity (Fuhlendorf *et al.* 2008). However the strength of the "magnet effect" can vary depending on factors such as the relative palatability and landscape context of burnt and unburnt vegetation (Kirkpatrick *et al.* 2011, Styger *et al.* 2011).

While fire can influence patterns of grazing, the converse is also true. Where grazing intensity is sufficient to form grazing lawns, fuel loads may be maintained at such low levels that fire is rarely possible (Leonard *et al.* 2010). However, in grasslands dominated by unpalatable tussock grasses, selective grazing of comparatively palatable new growth can elevate dead fuel levels and therefore increase the likelihood of fire. When fire occurs in such systems, intensive post-fire grazing can cause grassland to shift from the unpalatable and flammable tussock state to the palatable, rarely burnable lawn state (Kirkpatrick *et al.* 2011, 2016). Conversely, a decrease in grazing intensity, for example due to population decline in grazers in response to disease, predation or other factors, could lead to a vegetation transition in the opposite direction.

Fire and grazing may have synergistic effects on grassland vegetation. For example, in North American prairie, plant species richness was found to be higher in grassland where fire and grazing co-occurred compared to grassland subject to either disturbance alone (Collins & Barber 1985).

The combination of fire and grazing may be effective in preventing tree or shrub invasion of grassland where either disturbance alone would not have this effect (Kirkpatrick 2004). An example of the potential negative consequences of the combination of fire and grazing is the Central Plateau, where frequent burning and overgrazing by sheep resulted in severe sheet erosion and the transformation of grassland into shrubland (Jackson 1973, Kirkpatrick & Duncan 1987).

DISTURBANCE IN TASMANIAN HIGHLAND GRASSLANDS

Grazing

Grazing and fire are the major disturbances in Tasmanian highland grasslands. Grazing by Bennett's Wallabies, Common Wombats (*Vombatus ursinus* Shaw, 1800) and (below 1000 m) Tasmanian Pademelons (*Thylogale billardierii* Desmarest, 1822) is essentially ubiquitous in this vegetation. At some sites these species occur at high densities and remove considerable amounts of vegetation biomass (Leonard *et al.* 2010). Rabbits also occur in most grasslands. In addition, some areas are seasonally grazed by domestic stock, mainly cattle. Cattle and sheep grazing in highland grasslands was common in the nineteenth and twentieth centuries (Shepherd 1973). Highland sheep grazing largely ended when the Tasmanian Wilderness World Heritage Area was extended to include the eastern Central Plateau in 1989 (Kirkpatrick 2007). Cattle grazing has also gradually declined, but is still practised in a number of locations, including grasslands with high conservation value (e.g., Vale of Belvoir, Lees Paddocks). Bridle & Kirkpatrick (1999) found that sheep had greater impacts on the vegetation than rabbits and native herbivores. Where cattle are grazed at low density, they appear not to have severe negative effects on grassland vegetation, but do negatively affect associated wetland areas through pugging and erosion (Tengia *et al.* 2016).

In the absence of grazing, highland grasslands below 1000 m asl conform to the generally observed pattern of increasing dominance by tussock-forming grasses, with a concomitant decline in species richness as smaller-statured species are outcompeted (Gibson & Kirkpatrick 1989). However, this process may be less pronounced than in other grassy systems, such as lowland *Themeda* grasslands, due to the relative unpalatability of *Poa* (Leonard *et al.* 2010). In addition, a number of palatable native (e.g., *Microseris lanceolata* (Walp.) Sch.Bip., *Craspedia* spp.) and exotic (e.g., *Hypochaeris radicata* L.) taxa, and tall forbs generally, occur more frequently when grazing is removed (Bridle & Kirkpatrick 1999). Many of these species also produce more flowers in the absence of grazing, and therefore their reduced occurrence in grazed grassland may be a result of both direct predation and indirect effects on reproductive success (Bridle & Kirkpatrick 2001). Grazing also reduces shrub cover (Gibson & Kirkpatrick 1989) and eucalypt seedling establishment (Fensham & Kirkpatrick 1992) and so may be important in preventing a transition to shrubland or woodland (Kirkpatrick *et al.* 2016).

The maintenance of inter-tussock spaces and the creation of bare ground by grazers provides regeneration niches for a number of highland grassland forb species, including the nationally endangered *Leucochrysum albicans albicans* (A.Cunn.) Paul G.Wilson (Gilfedder & Kirkpatrick 1994). However overgrazing by stock (combined with fire) produced severe sheet erosion and a transition to shrubland on the Central Plateau (Jackson 1973, Kirkpatrick & Duncan 1987). These negative impacts of grazing are most pronounced in grasslands above 1000 m, where vegetation recovery from disturbance is extremely slow (Gibson & Kirkpatrick 1989, Bridle *et al.* 2001, Kirkpatrick & Bridle 2013). This slow recovery and associated soil erosion is exacerbated by frost heave in soils exposed by vegetation removal, which in turn is most severe in areas of relatively low rainfall (e.g., eastern Central Plateau), due to shorter periods of snow lie (Cullen 1995).

Fire

Historical and archaeological sources indicate that burning by Tasmanian Aboriginal peoples has been a key driver of vegetation patterns (Moss *et al.* 2007, Fletcher & Thomas 2010). There is considerable evidence that in western Tasmania, Aboriginal burning was instrumental in the maintenance of buttongrass moorland in areas climatically capable of supporting rainforest (Jackson 1968, di Folco & Kirkpatrick 2013). Similarly, analysis of fire scars on *Athrotaxis cupressoides* D.Don on the Central Plateau indicates that Indigenous Tasmanians applied patchy, low intensity fire to grassy vegetation in this area, with the fire return interval estimated to be 22–24 years (Holz *et al.* 2015). In addition, there is evidence that Indigenous burning was instrumental in maintaining the treelessness of highland grasslands occurring within a forest matrix. In the case of Paradise Plains, a grassland surrounded by rainforest in northeastern Tasmania, the presence of burnt *Nothofagus* logs dating from the pre-European era suggests that Aboriginal burning extended, if not created, this grassland (Ellis 1985). Similarly, the invasion of grasslands by fire-sensitive shrubs in the period since European colonisation also suggests the role of Aboriginal burning in previously excluding woody species (Bowman *et al.* 2012). Where the main woody invader is the serotinous obligate seeder *Leptospermum lanigerum* (Sol. ex Aiton) Sm., it can be inferred that such burning occurred at intervals less than the eight years it takes this species to reach reproductive maturity (Wood *et al.* 2017).

However burning alone cannot account for the exclusion of fire-tolerant sclerophyllous species from grassland, where these species are present nearby (Fensham & Fairfax 2006). Fensham & Kirkpatrick (1992) found that competitive exclusion by grasses was key factor in preventing woody invasion of highland grasslands. Soils may also play a role in causing treelessness. Lunt (1997c) found that the distribution of grassland on the Gippsland plain in Victoria closely matched that of flat plains with clay loam

soils, and ascribed the absence of trees from these areas to the combined effects of winter waterlogging and summer drought. In Tasmania, where vegetation and geological boundaries are closely congruent (such as the Vale of Belvoir), the occurrence of grasslands may similarly be a product of soil properties. Soil properties may also play a role in feedbacks between plant growth rates and fire regimes, which in turn influence grassland/forest boundary dynamics (Wood *et al.* 2017).

Graziers and hunters have used fire to manage highland grasslands since the 1820s, and it is possible that their practices were learnt from Indigenous Tasmanians (Cubit 1996, Holz *et al.* 2014). The aim of burning in the high country was to produce palatable feed for stock and game (Kirkpatrick & Bridle 2013). Fires were generally lit in early spring (when highland grassland has a high proportion of frost-killed dead foliage and is most flammable (Leonard 2009) such that fresh growth was produced in the following summer. In the more productive grasslands below 1000 m, patches were burnt rotationally with a typical inter-fire interval of 2–4 years (Cubit 1996, Wood *et al.* 2016). Examination of areas burnt recently by graziers indicate that these fires result in fine-grained patchiness of burn severity, including the occurrence of unburnt patches, reflecting variation in fuel curing and load (S. Leonard pers. obs.).

Tasmanian highland grasslands below 1000 m asl exhibit the general pattern of grass biomass removal by fire facilitating the persistence of interstitial species (Ferguson *et al.* 2009, Kirkpatrick *et al.* 2016). Kirkpatrick & Balmer (1991) suggested that the prolonged absence of fire from grassland at Cradle Valley resulted in a decline in forb abundance. The removal of fire from highland grasslands may also lead to the accumulation of peat, which in turn may facilitate a transition to sedgeland (Kirkpatrick 1991). Bare ground created by fire may provide niches for woody plant establishment (Fensham & Kirkpatrick 1992). In the absence of grazing this would result in succession to shrubland or woodland (Kirkpatrick 2004), however this is unlikely in almost all Tasmanian highland grassland, which is grazed by native animals. Conversely, the unpalatable shrub *Richea acerosa* can come to dominate grassy vegetation when fire is absent and grazing pressure relatively high (Kirkpatrick & Bridle 2016). However, as noted above, frequent firing and heavy grazing has led to shrub invasion on the Central Plateau. These observations highlight the complexity and unpredictability of responses that may arise due to changes in disturbance regimes in highland grasslands, particularly where disturbances interact (Kirkpatrick *et al.* 2011).

Grazing of highland grassland in the wake of fire may bring about a transition from a tussock-dominated structure to grazing lawn (Leonard *et al.* 2010, Kirkpatrick *et al.* 2011). It is possible that subsequent fires within a grassland will cause grazers to abandon existing lawns and concentrate on the newly burnt area, initiating the kind of shifting mosaic of grassland structure observed in North American prairie (Fuhlendorf & Engle 2004). However, in contrast to the prairies, Tasmanian grasslands occur as relatively small patches within extensive tracts of less palatable vegetation. This means that they are likely to be foci for grazing whether they are recently burnt or not (Kirkpatrick *et al.* 2011), and so the potential for a grazing-induced mosaic to form may be limited. Nonetheless, a number of highland grasslands exhibit a mix patches with lawn or tussock structure (Leonard *et al.* 2010) and future research to determine the relationships of such structural heterogeneity to fire and grazing regimes would be beneficial.

MANAGEMENT OF FIRE AND GRAZING IN TASMANIAN HIGHLAND GRASSLAND

There is ample evidence that a reduction in the biomass of dominant grasses through disturbance is necessary in order to maintain plant species diversity in Tasmanian highland grassland below 1000 m asl, as well as to prevent succession towards shrubland/forest or sedgeland (fig. 2). Grazing provides this to some degree, however the relative unpalatability of *Poa* means that grazing is likely to be concentrated on interstitial species rather than grass tussocks (Leonard *et al.* 2010). The ineffectiveness of native grazing alone in reducing *Poa* biomass is illustrated by the dense grass sward and low forb abundance in grasslands with large populations of wombats and wallabies, but a prolonged absence of fire (e.g., Cradle Valley; Kirkpatrick & Balmer 1991). Previous management-focused reviews have suggested that, in the absence of native grazers, stock grazing may be beneficial as a means of reducing grass biomass (Kirkpatrick 1991). However recent research has shown that low-density cattle grazing does not reduce tussock grass biomass in highland grassland (Leonard *et al.* 2010) and , while not having negative effects on grassland itself, does have negative effects on associated wetland areas through pugging and bank erosion (Tengia *et al.* 2016). Considering this, and the near ubiquity of native grazing, there would seem to be no ecological imperative for cattle grazing in highland grasslands.

The use of periodic fire is likely to be beneficial in managing highland grassland below 1000 m as it is an effective means of reducing *Poa* biomass (Kirkpatrick *et al.* 2011), creates regeneration niches for interstitial species and does not selectively consume these species (fig. 2.). Fire may also inhibit woody plant invasion (Bowman *et al.* 2013, Kirkpatrick & Bridle 2015, Wood *et al.* 2016). The combination of fire and grazing is also likely to increase floristic diversity and structural heterogeneity within grasslands through promoting the formation of grazing lawns (Leonard *et al.* 2010, Kirkpatrick *et al.* 2011, 2016). In addition, the juxtaposition of *Poa* tussocks and short grassland appears to be important in maintaining populations of the endangered Ptunarra Brown Butterfly (*Oreixenica ptunarra* L.E. Couchman, 1953; Neyland 1993, Bell 1999). Further research is required to precisely determine the appropriate fire regime(s) for maintaining biodiversity values in highland grassland. Examples of grasslands in good condition that have a history of

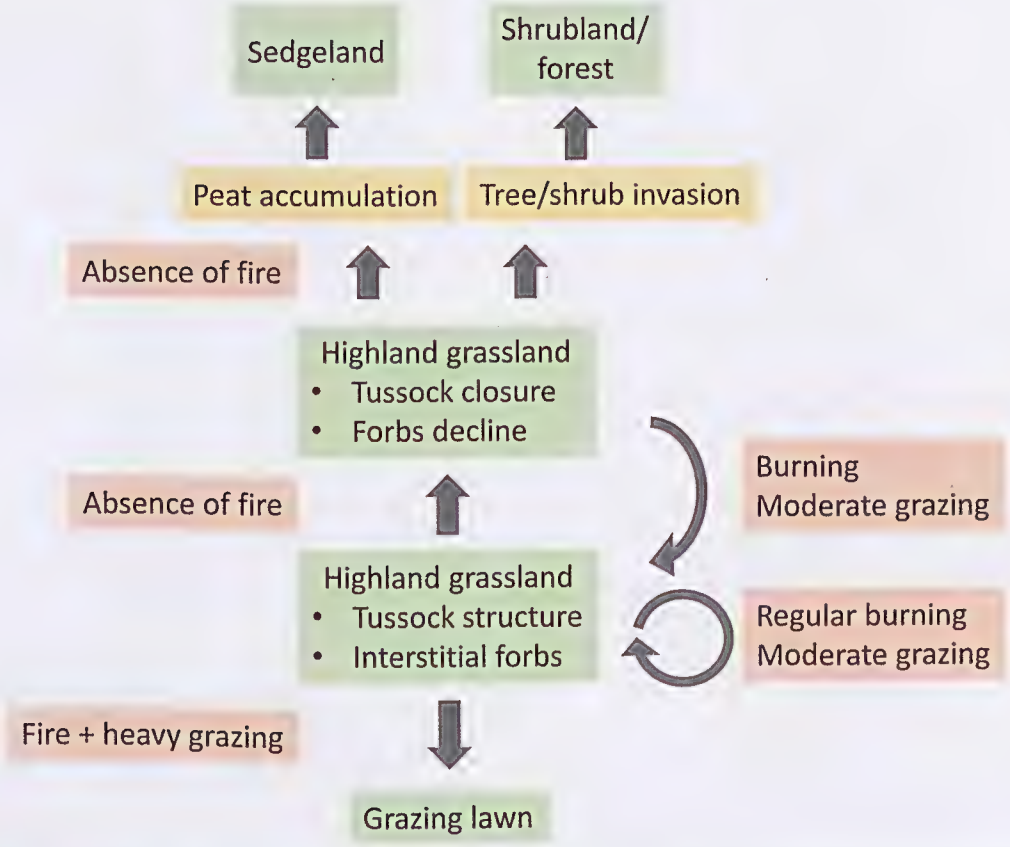

FIG. 2 — Summary of main transitions possible within Tasmanian highland grassland occurring below 1000 m asl in relation to variation in disturbance regimes. In the prolonged absence of fire grasslands typically exhibit accumulation of grass biomass, with concomitant decline in interstitial species. Absence of fire may also lead to tree/shrub invasion or peat accumulation, and eventual transition to shrubland/forest or sedgeland. Conversely, when fire is followed by heavy grazing, tussock grassland may be converted to lawn. Green boxes represent vegetation states, orange boxes disturbance regimes, and yellow boxes processes leading to vegetation transitions.

"traditional" burning by graziers, which may in turn be based on Indigenous practise, provide circumstantial evidence that such burning regimes are beneficial (Bowman *et al.* 2013, Wood *et al.* 2017). Where grasslands are threatened by invasion by fire sensitive shrubs, the vital attributes of the invading species may be able to be used to guide fire management.

In the low productivity environment above 1000 m asl, slow growth rates and grazing by native animals mean that competitive exclusion of interstitial species by grasses is unlikely to compromise floristic diversity (Gibson & Kirkpatrick 1989). There would appear to be no ecological need to apply disturbance to these higher altitude grassland, especially as large tracts are still undergoing the long process of recovery from past over-grazing and burning (Bridle *et al.* 2001, Kirkpatrick & Bridle 2013). Livestock grazing in particular is antithetical to ecological values in this vegetation.

Active management of highland grassland below 1000 m utilising periodic low intensity patch burning, in combination with native grazing (which is practically unavoidable in any case), is likely to be conducive to maintaining ecological values in this vegetation. Where such a management regime prevails there is no ecological imperative for cattle grazing. Above 1000 m active application of disturbance will seldom, if ever, be required. However, given that specific knowledge of optimal disturbance regimes for highland grassland is lacking, management should be accompanied by a well-designed monitoring program and the management strategy regularly reviewed.

ACKNOWLEDGEMENTS

Many thanks to Jamie Kirkpatrick and Jayne Balmer for comments on an earlier version of this paper. Dr Balmer also provided data on highland grassland extent and reservation.

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(Accepted 3 October 2017)

APPENDIX 1 – Systematic review of literature concerning fire and grazing in Tasmanian highland grasslands, published since 1999

Here we summarise the results of a systematic review of papers concerning fire and/or grazing in Tasmanian highland grasslands published in peer reviewed journals since the publication of Kirkpatrick (1999) (the last major review covering this vegetation). Relevant papers were identified by searching the Scopus and Web of Science literature databases using various combinations of the search terms "fire", "grazing", "Tasmania", "grassland", "grassy", "highland", "montane" and "alpine". Relevant papers were subjectively selected from search results, on the basis that they were focused on a) Tasmanian highland grasslands (alone, or in combination with other vegetation types), and b) fire and/or grazing. This process produced a list of 14 papers (see reference list above for full references). Six deal with effects of fire and grazing on flora and/or vegetation, three on grazing effects alone and two on fire effects alone. Two examine the process of woody invasion of grassland due to reduction in fire frequency, with one examining fire behaviour.

A number of "eras" or bodies of research are reflected in the results. Bridle & Kirkpatrick (1999, 2001) and Bridle *et al.* 2001 describe a series of studies of examining grazing effects and vegetation recovery following fire and over-grazing on the Central Plateau. Papers by Ferguson *et al.* (2009), Leonard (2009), Leonard *et al.* (2010) and Kirkpatrick *et al.* (2011, 2016) stem from a study of fire/grazing interactions in highland (and lowland) grassland, while Bowman *et al.* (2013) and Wood *et al.* (2017) examine landscape-scale vegetation change due to changed fire regimes. Discussion of the findings of these studies, and their implications for highland grassland management are included in the main body of the current paper.

Results of systematic review of papers concerning fire and/or grazing in Tasmanian highland grasslands published in peer reviewed journals since 1999

Author(s) & year	Topic
Leonard (2009)	Fire behaviour
Holz *et al.* (2015)	Fire effects, fire history
Kirkpatrick & Bridle (2013)	Fire effects, fire history
Bridle *et al.* (2001)	Fire/grazing effects
Ferguson *et al.* (2009)	Fire/grazing effects (on bryophytes)
Kirkpatrick & Bridle (2016)	Fire/grazing effects
Kirkpatrick *et al.* (2011)	Fire/grazing effects
Kirkpatrick *et al.* (2016)	Fire/grazing effects
Leonard *et al.* (2010)	Fire/grazing effects
Bridle & Kirkpatrick (1999)	Grazing effects
Bridle & Kirkpatrick (2001)	Grazing effects
Tengia *et al.* (2016)	Grazing effects
Bowman *et al.* (2013)	Vegetation change in relation to changed fire regimes
Wood *et al.* (2017)	Vegetation change in relation to changed fire regimes

NON-SEASONAL PLANT FOODS IN THE PALAWA (TASMANIAN ABORIGINAL) DIET: 1. THE YAM DAISY *MICROSERIS LANCEOLATA* (WALP.) SCH.BIP.

by Mike Macphail and David Woodward

with one text-figure and one plate

Macphail, M. & Woodward, D. 2017 (6:xii): Non-seasonal plant foods in the palawa (Tasmanian Aborigine) diet: 1: the Yam Daisy *Microseris lanceolata* (Walp.) Sch.Bip. *Papers and Proceedings of the Royal Society of Tasmania* 151: 11–18. ISSN 0080–4703.
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The tuberous roots of the Yam Daisy/murnong *Microseris lanceolata* were a staple plant food for Indigenous peoples in Victoria and New South Wales. In contrast, although the Yam Daisy occurs in Tasmania, it is not recorded as being eaten by the Tasmanian Aborigines (palawa) although fossil Liguliflorae pollen indicate that this perennial herb was growing here before European occupation in 1805. Unlike in Victoria up to the 1840s, as yet, there is no fossil evidence to show the species was sufficiently common to make a significant non-seasonal contribution to the palawan diet. However, assuming an adequate supply of the tubers, the palawa could have obtained energy from the modest content of simple sugars (via glycolysis) and its substantial content of fructans (prebiotics, converted to absorbable fatty acids by gut bacteria). Its sweet taste at certain seasons may have encouraged seasonal consumption. Recent research suggests that fructans may have health benefits, e.g., improved immune function; however, it seems improbable that the palawa specifically recognised those benefits.
Key Words: Indigenous non-seasonal plant foods, Tasmanian Aborigines, palawa, *Microseris lanceolata*, Yam Daisy, murnong, fossil pollen, carbohydrates, fructan, inulin

INTRODUCTION

The postulated high protein/low carbohydrate ("palaeo") diets that sustained traditional hunter-gatherer societies for millennia are a current focus in the anthropological literature as well as in the "food fad" culture (www.meltorganic.com/the-paleo-diet-real-or-fad/ (accessed 20 April 2017)). An Australian example of the former is the study of over 800 Indigenous plant foods, which concluded that the traditional diet was high in dietary fibre but relatively low in available carbohydrates, with over half being sugars derived from fruit and honey (Brand-Miller & Holt 1998). More generally, Cordain *et al.* (2000) and Ströhle & Hahn (2011) have demonstrated that the diets of modern hunter-gatherers vary markedly in their carbohydrate content but, whenever and wherever it is ecologically possible, >50% of their subsistence is derived from animal foods.

Whether a diet that is extremely restricted in carbohydrates is harmful to human health, is uncertain (compare Westman 2002, Cummings & Mann 2012). However, this will not have been a concern for First Peoples living in environments where fruit, nuts, seeds and honey provide a year-round source of carbohydrate but might have been for the palawa (Tasmanian Aborigines) living on the mid-high latitude island of Tasmania with its rich fauna but depauperate edible flora and short plant-growing season (see Monroe 2014).

Precisely which native plant foods in Tasmania were exploited by the palawa has been debated since the 1830s, partly due to the limited documentary evidence (see reviews by Noetling 1910, Hiatt 1967, Cane *et al.* 1979, Ryan 1981, Woodward *et al.* 1987, Plomley & Cameron 1993) and partly because the macrofossil remains of edible plants are rarely if ever preserved in Indigenous cultural deposits, unlike faunal remains (compare Lourandos 1968, Garvey 2007, 2011).

This is the first of two short papers reviewing the microfossil (pollen and spore) evidence for edible plants that potentially provided a non-seasonal source of food for the palawa before European occupation of Tasmania in 1805. The edible species discussed here is the Yam Daisy *Microseris lanceolata* (Walp.) Sch.Bip., a perennial herb (forb) species now found growing in open habitats that are free from grazing across much of southern and eastern mainland Australia and lowland Tasmania except the South-West (avh.ala.org.au/occurrences/search?taxa=Microseris+lanceolata#tab_mapView (accessed 28 November 2016)).

BACKGROUND

The tuberous roots (tubers) of the Yam Daisy are widely considered to have been a staple Indigenous food in mainland Australia (Gott 1982, 1983, 2016) but were not amongst the edible plants in Tasmania witnessed being eaten (or assumed to have been eaten) by the palawa by early nineteenth century observers such as the "protector of the Aborigines" George Augustus Robinson (1791–1866) (compare Anon 1834, Gunn 1842, Backhouse 1843, Plomley 2008). A search of newspapers prior to 1850 via

Trove (trove.nla.gov.au/(accessed 2016-2017)) has failed to uncover any additional record that might indicate *Microseris lanceolata* was eaten by the palawa; the earliest herbarium specimens of *M. lanceolata* in Tasmania date to 1840s (M. de Salas pers comm.). This contrasts with the recent proposal (Romanin *et al.* 2016) that fossil pollen of the type (Liguliflorae) produced by *M. lanceolata* at Diprose Lagoon in the northern Midlands are evidence that the Yam Daisy was an important root vegetable in the palawa diet before European settlement of the district in the early 1820s and presumably also before European occupation of the State in 1805.

Key issues are: (1) How reliable is the Colonial period ethnographic evidence? (2) Can fossil pollen grains produced by *M. lanceolata* be distinguished from the morphologically very similar pollen produced by other native and introduced species within the tribe Liguliflorae (synonyms Cichorieae, Lactuceae) of the cosmopolitan daisy/daisy-bush family Asteraceae, in particular the large numbers of introduced widely naturalised "weed" Liguliflorae in Tasmania (see Curtis 1963, Gott 1983)? (3) Are relative abundances of fossil Liguliflorae pollen adequate to show the Yam Daisy *M. lanceolata* was growing in large numbers in the Midlands before the 1820s (see Romanin *et al.* 2016)? (4) Are there alternative reasons why the daisy might have been eaten other than as a source of energy?

In examining these issues we emphasise that, unlike mainland Australia, all Liguliflorae in Tasmania are introduced species except for *M. lanceolata* and a native dandelion, *Taraxacum aristum* G.Hagl. & Markl., that is confined to high elevation sites on the Central Plateau (figs 1a, 1b).

MICROSERIS LANCEOLATA (Walp.) Sch.Bip.

Microseris lanceolata is a summer-dormant perennial forb up to 40 cm tall that differs from herbs such as the sedges and grasses in having a rosette of broad/flat rather than narrow/linear leaves. The fleshy tuberous root used by the species to store carbohydrate is edible, can be eaten cooked or raw, and was observed to be harvested by Indigenous people in southwest Victoria in 1840 (Gott 1982, 1983). Numerous geographic variants are recorded. For example, the Tasmanian species is markedly smaller than the mainland Australian form (Gott 1982). The tuberous root in Victorian populations varies from "radish-like" in shallow rocky soil, branched and "rather fibrous" under alpine conditions, and "more carrot-like and tapering" in the lowlands (Leigh & Mulham 1965, cited in Gott 1982).

Since reaching Australia and New Zealand, apparently some 2.6 million years ago (see Macphail 1999a, Partridge 1999, Vijverberg *et al.* 1999), *Microseris* has evolved into four morphologically distinct ecotypes categorised as "alpine", "murnong", "fine pappus" and "coastal" (Vijverberg *et al.* 2000). The latter two ecotypes now are considered to represent a separate species, which is endemic to New Zealand [*Microseris scapigera* (Sol. ex A.Cunn) Sch. Bip.], although in the past Tasmanian specimens were also assigned to this species (compare Curtis 1963 p. 381, Sneddon 1977). With reservations (see vro.agriculture.vic.gov.au/dpi/vro/vrosite.nsf/pages/sip_salt_native_yam (accessed 28 February 2017)), the "alpine" and "murnong" ecotypes are assigned to the one species *M. lanceolata* that is endemic to Australia despite the differing ecologies. For example, the "alpine" ecotype is restricted to elevations above 1000 m in the mountains in southeast Australia whilst the "murnong" ecotype is only found in lowland habitats. In contrast, introduced Liguliflorae species are very widely naturalised at most elevations, including in Tasmania, and occur in grazed agricultural land, disturbed and undisturbed open forests and on roadsides. We note this near-ubiquitous distribution is poorly reflected in herbarium collections.

Modern pollen

Distinguishing pollen of native Liguliflorae such as *M. lanceolata* from pollen of the widely naturalised "weed" genera such as *Crepis* (Hawk's Beard), *Hypochaeris* (Cat's Ear) *Sonchus* (Sowthistle) and *Taraxacum* (Common Dandelion) is difficult using characters visible under bright field microscopy. For example, all Liguliflorae pollen types are characterised by a cell wall (exine) in which the outer layer (sexine) is raised in a pattern of ridges (lophae) surrounding a variable number of large, window-like (fenestrate) apertures (lacunae); the ridges are ornamented with single rows of spines (echinae) (see Punt *et al.* 2007). Moore *et al.* (1991) and Beug (2004) have divided the European genera into a number of morphotypes, e.g., *Crepis*-type, *Sonchus*-type and *Taraxacum*-type, but do not include *Microseris*. At present it is uncertain which, if any, of these morphological classes would best accommodate modern (or fossil) pollen of *M. lanceolata* (compare Fig. 2, Plate 57 in Moar 1993) (pl. 1).

Fossil pollen

Fossil Liguliflorae pollen have been recorded on Colonial period archaeological sites in southeast mainland Australia and Tasmania and sporadically in lake sediments and peat in Tasmania that post-date European settlement (Macphail 1999b, 2001, 2016, Macphail & Casey, 2008, M.K. Macphail unpubl. data). One exception in Tasmania is Hazards Lagoon on the Freycinet Peninsula on the East Coast, where Mackenzie & Moss (2014) have recorded trace numbers of fossil Liguliflorae pollen in sediments broadly dated to the middle Holocene ca. six thousand (kyr) years ago, and Late Pleistocene ca. 11–18 kyr ago (fig. 1c). A second (unpublished) record is Liguliflorae pollen in ca. 1.5 kyr old peat at the Skullbone Plain Reserve above 1100 m elevation on the western side of the Central Plateau (F. Hopf pers.comm.) although here the source could be *Taraxacum aristum*. As far as is known, Diprose Lagoon (41°48'S 147°22'E) at Cleveland in the northern Midlands is the only published site where Liguliflorae pollen have been found in significant numbers (4%) in independently-dated sediments that accumulated in the period between the European settlement of the Midlands in the 1820s

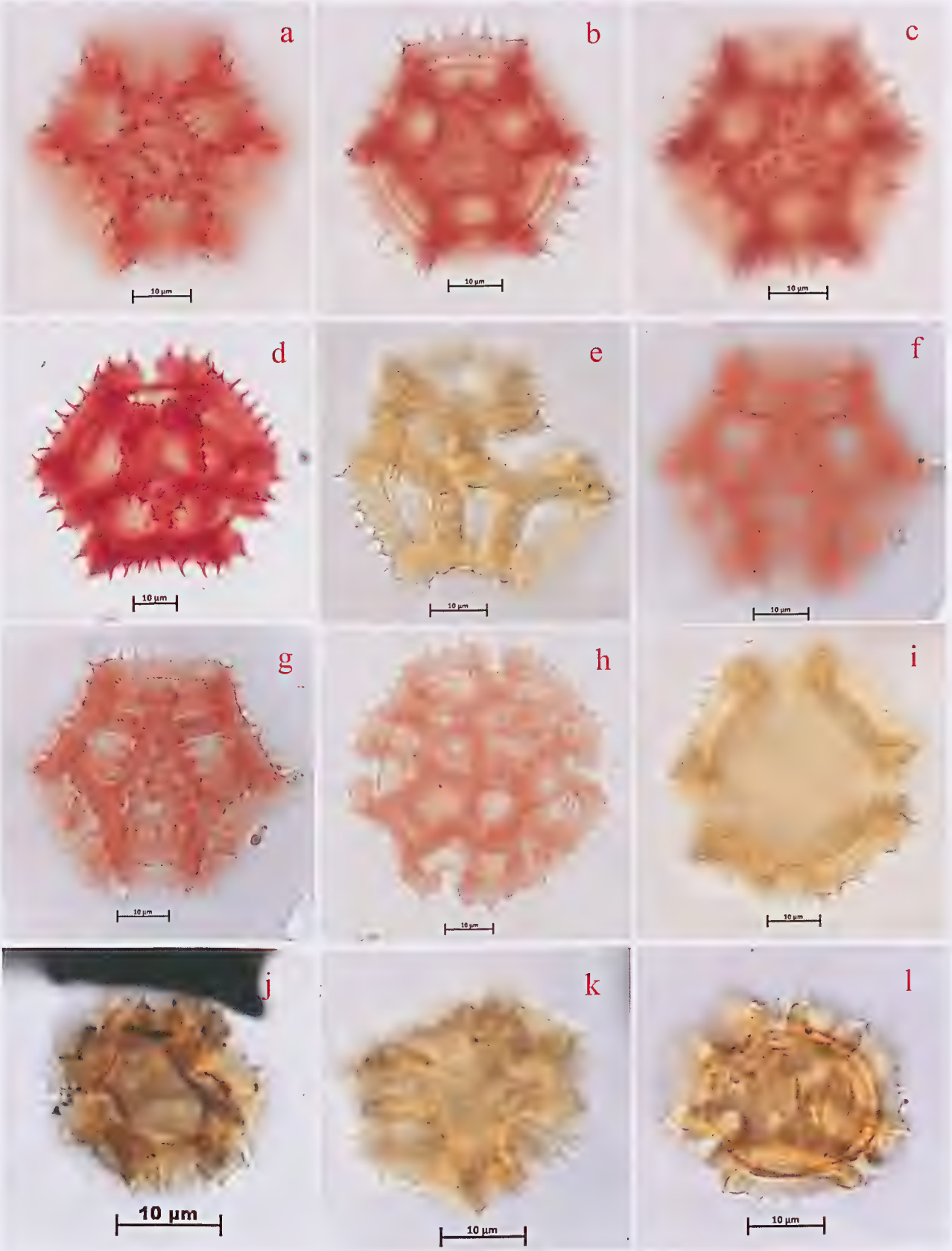

PLATE 1 — Modern Liguliflorae pollen. a–c: *Microseris lanceolata* (Walp.) Sch.Bip. pollen in high median and low optical view (coll. Rodway Herbarium 1969). d: *Cichorium intybus* L. (Chicory) pollen in median optical view (cultivated, New South Wales). e: *Lactuca sativa* L. (Lettuce) pollen in median optical view (cultivated, New South Wales). f–h: *Taraxacum officinale* Weber (Common Dandelion) pollen in high and median optical view (naturalised, New South Wales). i: *Sonchus asper* (L.) Hill (Prickly Sowthistle) pollen in median optical view (naturalised, New South Wales). j: fossil Liguliflorae pollen in median polar view (specimen from a bag of charred grain, Barangaroo Historical Archaeological Site, Sydney ca. 1860). k–l: fossil Liguliflorae pollen in median polar view (specimens preserved in buried soils, Montpelier Retreat Historical Archaeological Site, Hobart, 1805–1823). Differences in pollen size reflect differences in processing techniques and swelling of the modern grains over time.

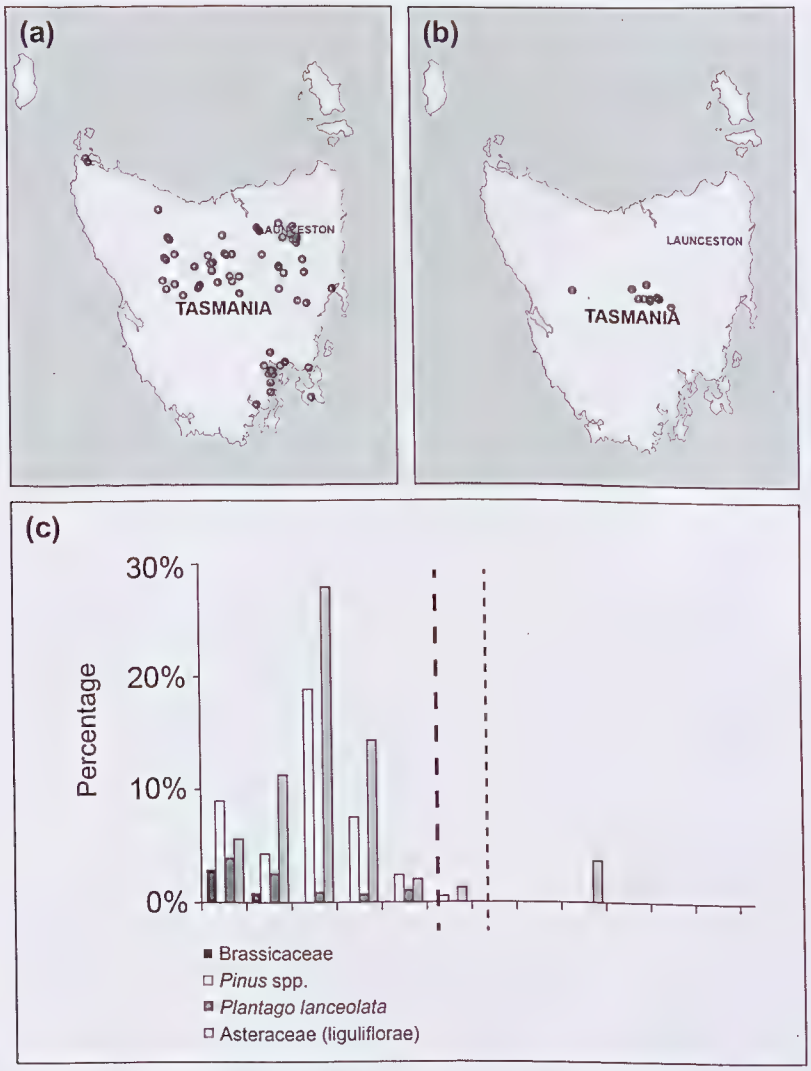

FIG. 1 — (a) Distribution of *Microseris lanceolata* in Tasmania; (b) distribution of *Taraxacum aristum* in Tasmania; (c) relative pollen abundance of pine (*Pinus*), *Microseris*-type (Liguliflorae) and other herbs such as the crucifers (Brassicaceae) and European Plaintain (*Plantago lanceolata*) that are typically associated with European agricultural activity in the Midlands of Tasmania. The coarse-dashed vertical line (LHS) indicates the depth the first grain of *Pinus* pollen was found; the fine-dashed vertical line (RHS) indicates the approximate date that Europeans arrived in Tasmania. The *x*-axis is graduated in 2 cm intervals from the surface sediment on the left to 24 cm depth on the right.

and Tasmania as a whole in 1805 (Romanin *et al.* 2016). In contrast, relative abundances of Liguliflorae pollen at the same site attain values of up to 28% in sediments that post-date ca. 1820.

DISCUSSION

Which plant foods actually were eaten by the palawa is debatable given that (1) only a limited number of accounts date to the early to mid nineteenth century when the traditional culture was still being maintained in Tasmania and (2) a number of these accounts almost certainly were subject to observer biases (including gender bias). Similarly, occurrences of fossil Liguliflorae pollen in sediments that pre-date European settlement of Tasmania are not in themselves unequivocal evidence that the source species was *Microseris lanceolata* or that this edible plant was sufficiently abundant to be a food resource. A third *caveat* is that a food resource can be abundant but, for cultural reasons, may not have been exploited by the palawa, e.g., bony fish over the past three ka (compare Gunn 1842, Jones 1978, Rowland 1983, Low 1988, Taylor 2007). These issues are discussed below:

1. How reliable is the Colonial ethnographic evidence?

Plomley & Cameron (1993 p. 2) caution against the assumption that, "because a plant was used as food by [mainland] Australian Aborigines it was therefore so used by the Tasmanian Aborigines". Although G.A. Robinson and J. Backhouse were familiar with the Yam Daisy and record the species being harvested by Aboriginal women in Victoria in the 1840s (see Backhouse 1843, Gott 1983), there is no evidence that these observers were familiar with it as an Indigenous food in Tasmania or their observations were biased against "women's work". Observer bias,

however, remains a problem when interpreting other Tasmanian Colonial records. An example is the different importance attached to particular plant foods. At one extreme is Backhouse (1843) who comments their food consisted mainly of roots and some species of fungus, but subsequently included tree-fern stems (species not stated) and the "root" (rhizome) of the common bracken fern *Pteridium esculentum* (G.Forst.) Cockayne. In contrast, Davies (1846 p. 79) downplays the role of plants, describing the native bread or "truffle" [*Laccocephalum mylittae* (Cooke & Masse) Nuúñez & Ryvarden] as "the only vegetable production they use" even though he later mentions "parts of the tree-fern" (again species not stated) and "grass-tree" (presumably *Xanthorrhoea australis* R.Br.). The debate regarding Indigenous plant foods is further complicated by (i) the uncertain identity of many plants cited in the Colonial documents and (ii) a failure to state explicitly which plants had been seen to be consumed, as opposed to those that might have been eaten, e.g., Gunn (1842).

An equally relevant issue is that the Yam Daisy is highly palatable to stock (Gott 1983) and therefore any observations made in the Midlands in the 1830s–1840s are likely to postdate massive decimation of the species by the large sheep population (estimated to number ca. 182 000 as early as 1820: Boyce 2010) over the preceding one to two decades. For these reasons, a cautious assessment is the early Colonial ethnographic observations are useful working hypotheses, rather than firm evidence that particular species such as *Microseris lanceolata* were or were not eaten by the palawa.

2. Can *Microseris lanceolata* pollen be distinguished from other Liguliflorae species and was the species sufficiently common in Tasmania to have been a staple food resource?

If, as appears to be the case, the Diprose Lagoon specimens are *in situ*, then it is almost certain that the fossil Liguliflorae pollen at 17 cm depth represents *M. lanceolata*, not *Taraxacum aristum* or an introduced Liguliflorae species (fig. 1c). Reasons for this are the lowland setting (191 m elevation) and, as far as is known, the absence of other extant or extinct native Liguliflorae species in the Tasmanian Midlands. In contrast, relative pollen abundances of up to 28% that post-date the first occurrence of *Pinus* pollen almost certainly represent one of the widely naturalised exotic "weed" Liguliflorae, e.g., the Common Dandelion *T. officinale*. Circumstantial support for the latter interpretation is provided by the increased relative abundance of Liguliflorae pollen, which is mirrored by (i) an increase in other definite and probably introduced agricultural "weeds" such *Plantago lanceolata* (European Plantain), Brassicaceae, (crucifers) and *Rumex* (docks) and (ii) a decrease in relative abundance of native herbs such as Chenopodiaceae (samphires/salt-bush) and Asteraceae subfamily Tubuliflorae, as well as tree genera such as *Allocasuarina/Casuarina*, (she-oaks) and *Eucalyptus sensu lato* (eucalypts). The latter trend reflects European clearing of the mosaic of grasslands and dry sclerophyll woodland (savanna woodland) that had dominated the Midlands for most of the Holocene (compare Macphail & Jackson 1978, Sigleo & Colhoun 1981, Fensham 1989, Fensham & Kirkpatrick 1989). Accordingly Romanin *et al.'s* (2016) interpretation that *M. lanceolata* was growing in savanna grasslands in the Midlands (and therefore might have been a food resource) before ca. 1820 appears well-supported.

The related question of abundance is less straightforward although data from southeast mainland Australia concerning the production and dispersal of Liguliflorae pollen and their relative abundance in modern and pre-European sediments are available for comparison. For example, modern pollen data from pollen traps, surface sediments and buried soils on archaeological sites, including in Tasmania, indicate that Liguliflorae pollen are produced in large amounts but these grains are only transported short distances away from the parent plants (Dodson 1983, Kershaw *et al.* 1994, Macphail 1999b, 2016, Macphail & Casey 2008, M.K. Macphail unpubl. data). Similar relative abundances of fossil pollen are recorded at coastal sites in southwest Victoria, a region where "millions of murnong [occurred] all over the plains" in 1840 (Robinson 1840, cited in Gott 1982 p. 64). Closer to the coast, relative abundances of Liguliflorae pollen vary from trace to <10% in mid-late Holocene swamp sediments in the Cape Bridgewater–Discovery Bay district but reach 60% in the nearby Bridgewater caves (Head no date, 1988). On the wider geographic scale, Liguliflorae pollen are found in trace to frequent numbers (>10%) in modern surface samples in southern New South Wales and in larger numbers in deposits where the parent plants are likely to have been growing on the site. However, the pollen type was not recorded in a survey of modern and pre-European settlement sediments in southeast Australia (Kershaw *et al.* 1994). Accordingly, the comparatively low value (4%) of Liguliflorae pollen recorded in Diprose Lagoon before ca. 1820 is unlikely to represent extensive populations of *M. lanceolata* in the surrounding landscape. By extrapolation, the Yam Daisy is not likely to have been a staple plant food resource in the northern Midlands although this may not have been the case elsewhere in Tasmania. For example we note that an entry for possible *M. lanceolata* (cited as *Scorzonera lawrencii* Hook.) collected by R.C. Gunn and now housed in the Kew Herbarium, UK, cites the species as being "Hab. Abundant" (Hooker 1847 p. 124; http://specimens.kew.org/herbarium/K000796798 (accessed 20 April 2017)).

3. Factors that may have influenced palawa consumption of *Microseris*

Whilst the distribution and population densities will have a critical factor in the availability of the Yam Daisy, we recognise other influences potentially might have been important in determining whether the tubers were consumed. These are food "taboos", "convenience of collection", the "sweet taste" and biomedical considerations.

Food taboos: The utilisation of plants, especially trees, can be subject to cultural restrictions (see Meyer-Rochow 2009). Whether the consumption of *Microseris lanceolata* by the palawa was subject to cultural dictates as has been

proposed for bony fish (compare Jones 1978, Taylor 2007) is unknown.

Convenience: Mainland (mainly Victorian) sources indicate that the tubers were easy to collect and could be eaten raw or cooked (Gott 1983), but the Tasmanian variety has smaller tubers (Gott 1982), which may have required more effort to collect.

Sweet taste: Europeans who have eaten the tubers have commented on the "radish-like" and "sweet" taste of the tubers (see Cribb & Cribb 1976). The latter characteristic is likely to reflect the substantial amounts of fructans (fructose polymers, in particular inulin), and modest amounts of simple mono- and di-saccharide sugars (mainly fructose and glucose). There is some evidence that in autumn the fructan level declines and the level of simple sugars increases (Incoll *et al.* 1989, Gott 1983). Since simple sugars are much sweeter than fructans, the seasonal variation in composition might explain the inconsistent reporting of sweetness and also the reported (Gott 1983) seasonal variations in Yam Daisy consumption by indigenous Victorians.

Biomedical considerations: With the exception of the Jerusalem Artichoke (*Helianthus tuberosus* L.) and Garlic (*Allium sativum* L.), the few samples of *Microseris lanceolata* tubers analysed to date have been found to have fructan concentrations that are substantially higher than any of the fruits and vegetables in the current "western" diet in Australia (Muir *et al.* 2007). Although fructans per se cannot be digested by enzymes secreted by the human gastrointestinal tract, inulin-rich foods are prebiotics, stimulating the proliferation of specific bacteria in the large intestine and have distinctive health properties. For example, these bacteria convert fructans to short-chain fatty acids, which when taken up by colon mucosal cells are postulated to produce an enhanced immune response (Roberfroid 2005). Whether the palawa (or, indeed, indigenous mainlanders) attributed any specific health impacts to the Yam Daisy or other inulin-rich plant foods is beyond the scope of this paper (compare Brand Miller *et al.* 1998).

CONCLUSIONS

We conclude that there is as yet no unequivocal evidence, either palynological or ethnographic, that *Microseris lanceolata* grew in significant numbers in Tasmania prior to European settlement to give the species the "staple plant food" status claimed for the Yam Daisy in Victoria (compare Bowdler 1981). This, however, does not preclude the indigenous consumption of the Yam Daisy in Tasmania, possibly for other cultural reasons such as the seasonal variation in availability and its sweet taste. If so, it was probably on a limited scale, as the recorded palawa vocabularies do not include any word associated with "roots" that can be identified with the Yam Daisy (compare Plomley 1976, Gott 1983). Whilst the tubers (at least the Victorian variety) have some compositional features, such as a high fructan content, that might provide ancillary health benefits (Kolida & Gibson 2007, Leach 2007, Slavin 2013), it seems unlikely to assume that this aspect would have influenced its consumption by palawa.

ACKNOWLEDGEMENTS

Dr Miguel de Salas, Tasmanian Herbarium, Tasmanian Museum and Art Gallery, Hobart provided valuable comment on early Colonial period herbarium records. CSIRO Publishing gave permission to reproduce Figure 2e in Romanin *et al.* (2016). This diagram was redrafted by Tara Macphail as part of fig. 1 for the purposes of this paper. All are gratefully thanked.

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(accepted 3 October 2017)

THE FRESHWATER FAUNA OF THE SOUTH POLAR REGION: A 140-YEAR REVIEW.

by Herbert J.G. Dartnall

(with one text-figure, one table and one appendix)

Dartnall, H.J.G. 2017 (6:xii): The freshwater fauna of the South Polar Region: A 140-year review. *Papers and Proceedings of the Royal Society of Tasmania* 151: 19–57. ISSN 0080-4703. Department of Biological Sciences, Macquarie University, Sydney, NSW, 2109 Australia. E-mail: herbdartnall@pip.com.au

The metazoan fauna of Antarctic and sub-Antarctic freshwaters is reviewed. Almost 400 species, notably rotifers, tardigrades and crustaceans have been identified. Sponges, molluscs, amphibians, reptiles and fishes are absent though salmonid fishes have been successfully introduced on some of the sub-Antarctic islands. Other alien introductions include insects (Chironomidae) and annelid worms (Oligochaeta). The fauna is predominately benthic in habitat and becomes increasingly depauperate at higher latitudes. Endemic species are known but only a few are widely distributed. Planktonic species are rare and only one parasitic species has been noted.
Keywords: freshwater, fauna, Antarctica, sub-Antarctic Islands, maritime Antarctic, continental Antarctica.

INTRODUCTION

The first collections of Antarctic freshwater invertebrates were made during the "Transit of Venus" expeditions of 1874 (Brady 1875, 1879, Studer 1878). Since then many Antarctic expeditions have collected limnological material as part of their scientific programs. The results of these surveys, which range from single-line observations to detailed reports, written in a number of languages, are scattered throughout the literature. The objective of this paper is to bring together these reports, to consider the validity of the identifications, to update the taxonomy where necessary, and assess the thoroughness of the sampling in order to both review current knowledge and highlight areas for future investigation.

Some definitions and limitations

The scope and limitations of this compilation are defined as follows. Within the context of this paper the Antarctic region is defined as the area approximately delimited by the Antarctic Polar Front Zone (APFZ), including the sub-Antarctic islands that lie on, or just to the north of, this front (fig. 1). The Antarctic region is divided into four distinct zones –

- the sub-Antarctic islands,
- the maritime Antarctic,
- the Antarctic coastal fringe, and
- the ice-covered centre of continental Antarctica.

The sub-Antarctic islands comprise the six groups of treeless Southern Ocean islands – South Georgia, the Prince Edward Islands, Îles Crozet, Îles Kerguelen, Heard Island and the McDonald Islands, and Macquarie Island – that lie on or just to the north of the Antarctic Polar Front. Here the vegetation is abundant and often waterlogged. Water bodies are common and include lakes, rivers and streams. [Note that the Falkland Islands and the islands to the south and east of New Zealand – namely Campbell, Auckland, Snares, Antipodes, Bounty, and Chatham islands – that some authorities label sub-Antarctic, are not included in this definition. While these cool-temperate islands have a similar verdant vegetation and numerous water bodies they are warmer and some are vegetated with woody shrubs and trees.]

The maritime Antarctic zone includes Graham Land, the Antarctic Peninsula north of the Antarctic Circle, as well as the off-lying island groups of the South Atlantic/ Weddell Sea including the South Shetland Islands, South Orkney Islands, South Sandwich Islands, and Bouvetøya (Bouvet Island), that are often enclosed by the maximum extent of the winter sea-ice. Lakes here are shallow and ice-covered for much of the year. Mosses and liverworts (bryophytes) and lichens are common and reasonably widespread, together with two flowering plants – the hair grass *Deschampsia antarctica* Desv. and the pearlwort *Colobanthus quitensis* (Kunth) Bartl.

The Antarctic coastal fringe, as its name implies, includes the narrow strip of land up to a couple of hundred kilometres wide around Continental Antarctica. Here, "oases" – areas of ice-free ground – occur, and bryophytes, lichens and algae can grow though are generally sparse. Rivers are ephemeral, lakes can be locally common and encompass landlocked fresh to hypersaline water bodies. Epishelf lakes are large bodies of fresh water floating on the sea and sandwiched between permanent ice shelves and coastal rock of both the maritime Antarctic and Antarctic coastal fringe. Proglacial lakes – meltwater bodies on the surface and alongside glaciers – are ultra-oligotrophic.

Surface lakes do not occur on the ice-covered centre of Antarctica. However, this area does support a number of subglacial lakes buried under thousands of metres of ice which are in the very early stage of investigation.

Many freshwater invertebrates can tolerate water of increased salinity, however, in this paper I do not consider water bodies with a salinity >5.5‰ after Dartnall (2000) who determined that this was the natural upper salinity tolerance of freshwater invertebrates in the Vestfold Hills. All permanent freshwater habitats – rivers and streams, wallows, pools, ponds, lagoons and lakes including epishelf, glacial and subglacial lakes that have a salinity of <5.5‰

will be considered. Casual water or soaks are not included as these areas of temporary standing water or flooded vegetation are considered to be terrestrial habitats. Similarly, species found in the intertidal zone or in pools just above the high tide mark, which are considered brackish, will not be included.

In the Antarctic (specifically the Antarctic coastal fringe and maritime Antarctic zone) pools are defined as shallow bodies of water that freeze solid in the winter and lakes as deeper bodies of water that do not. This is an important biological distinction often leading to quite separate floras and faunas. On the sub-Antarctic islands where it is not cold enough to cause even the smallest water bodies to freeze completely, the floras and faunas of the various water bodies are essentially similar; here the terms lake, lagoon, pool, pond and tarn are often applied arbitrarily. Fringing terrestrial vegetation can mask the edge of such water bodies so it is not always possible to determine where dry land ends and the lake begins.

This study is confined to metazoan groups and does not include the Protozoa. All truly freshwater species including those that only complete part of their life cycle aquatically will be included; while the validity of terrestrial and marine interlopers that drop in or are blown in and continue to function once immersed in freshwater will also be considered.

PRESENTATION OF THE RESULTS

Earlier reviews have divided the Antarctic continent into four or six segments considering the results from each 90° or 60° arc (Pugh 1993, Andrássy 1998, Pugh *et al.* 2002). In this paper I include the six sub-Antarctic island groups and track westwards from Macquarie Island to South Georgia picking up the intervening sub-Antarctic islands, before tracking southwards through the islands of the Scotia Arc and south along the Antarctic Peninsula then returning eastwards along the coast of the Antarctic continent to McMurdo Sound (fig. 1). This sequence, reflected in the order of columns in the table, not only keeps adjacent sampling locations together but broadly speaking follows a slow increase in latitude of the major freshwater sampling stations.

In figure 1 a solid red circle indicates the location of an area of particular interest. On the figure, the table and key references in the text **MqI** stands for Macquarie Island, **HI** is Heard Island, **K** is Îles Kerguelen, **C** is Îles Crozet, **PE** is Prince Edward Islands, **SG** is South Georgia, **SO** is South Orkney Islands, **SS** is South Shetland Islands, **AP** is Antarctic Peninsula, **Sch** is Schirmacher Oasis, **TH** is Thala Hills, **PCM** is the Prince Charles Mountains, **LH** is the Larsemann Hills, **VH** is the Vestfold Hills, **Has** is Haswell Island, **OH** is the Obruchev Hills, **BH** is the Bunger Hills, **WL** is Wilkes Land and **McM** is the McMurdo Sound region. Here McMurdo Sound is taken to include Ross Island and the Dry Valleys; the Antarctic Peninsula is taken to include Alexander Island and the southern end of the Peninsula (Palmer Land); while the South Shetland Islands also include the Argentine Islands and Graham Land, the northern tip of the Peninsula. Other locations where freshwater studies have been carried out but the results are too few to warrant a column of their own in the distribution tables are mentioned in the text.

The following symbols have specific meaning throughout the distribution table (see page 22):

+ the presence of a particular species at a given location
× an interloping terrestrial or brackish water species that has strayed into freshwater and continues alive in the "wrong" environment
‡ a record that warrants verification, based on an unexpected observation and/or very few specimens
? a questionable or dubious record
( ) an anthropogenic/introduced species
† a species that is no longer present or extinct at a location
numeral – the number of recognised but not identified taxa, e.g., "the collector noted three unidentified species of nematode"

Finally, the total number of identified species found at each location is given for some groups in the table though this may not represent a true "total" if there are multiple entries of unidentified or partially identified records. A blank entry indicates an absence of data. A zero ('0') indicates definitive or suspected absence of that group.

The Fauna

As is appropriate for this review only metazoan groups that are normally found in freshwater will be considered. Exclusively marine or terrestrial phyla, classes, orders and families are excluded (following the taxonomy as detailed in Anderson 2001).

Phylum: Porifera

There is just one mention of freshwater sponges in the Antarctic literature. Thomson (1895) reported that amongst the material of a sponge taken from a freshwater pool on Macquarie Island there were two very imperfectly preserved specimens of a species of calanoid copepod *Guernea antarctica*. He considered that this copepod, now known as *Boeckella brevicaudata* (see appendix 1 for a list of synonyms and mistaken identities) might have lived in the cavities of the sponge. *B. brevicaudata* is a free-swimming copepod that does not hide in crevices and Thomson is mistaken in implying his sponge is of freshwater origin. It undoubtedly came from the nearby inshore marine environment, probably dropped by a passing seabird. Consequently it is not a legitimate freshwater inhabitant.

Points of interest (Porifera)

No freshwater sponges have been reported from the Antarctic region.

Phylum: Cnidaria

The only record of a freshwater coelenterate from the Antarctic region is the green hydra reported from South Georgia by Headland (pers. comm.) (table 1: Cnidaria). With only one specimen seen in 1987 confirmation of

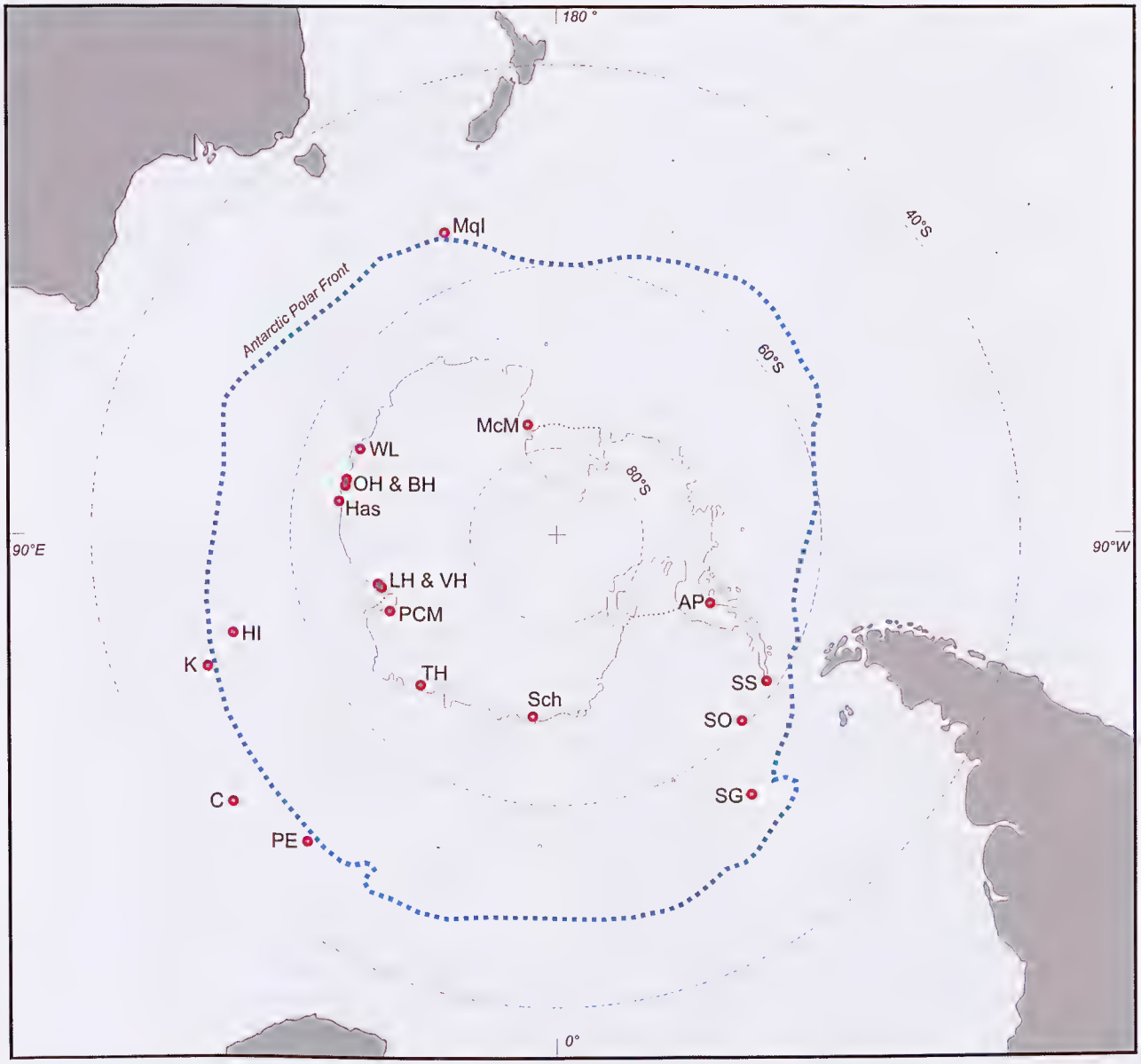

FIG. 1 — Map of the Antarctic and sub-Antarctic regions showing the Antarctic Polar Front (dotted blue line) and the locations where freshwater surveys have been made (red spots). On this map **Mql** is Macquarie Island, **HI** is Heard Island, **K** is Îles Kerguelen, **C** is Îles Crozet, **PE** is Prince Edward Islands, **SG** is South Georgia, **SO** is South Orkney Islands, **SS** is South Shetland Islands, **AP** is Antarctic Peninsula, **Sch** is Schirmacher Oasis, **TH** is Thala Hills, **PCM** is the Prince Charles Mountains, **LH** & **VH** is the Larsemann Hills and Vestfold Hills, **Has** is Haswell Island, **OH** & **BH** is the Obruchev Hills and Bunger Hills, **WL** is Wilkes Land and **McM** is the McMurdo Sound region including the Dry Valleys.

its continuing presence would be valuable. Note that the anthomedusa (*Rathkea lizzioides* O'Sullivan, 1984) reported from the Vestfold Hills by Bayly (1986) and Bayly & Eslake (1989) together with a ctenophore that was found in Lake Burton are not included in this study. These are marine species that have only been found in Lake Burton, a meromictic saline lake with a salinity of 40+‰ (Dartnall 2000) and consequently are not within the "freshwater limitations" of this survey.

Points of interest (Coelenterata)

Just one specimen of a green hydra has been reported from the Antarctic region at South Georgia. Confirmation of the continuing presence of this hydra would be valuable.

Phylum: Platyhelminthes

While no parasitic flatworms (Trematoda, Monogenea and Cestoda) have been reported from freshwater in the Antarctic region a few free-living species (Turbellaria) have been identified (table 1: Platyhelminthes). Poorly known and with patchy distributions, flatworms are nevertheless an important component of the freshwater ecosystem particularly on the sub-Antarctic islands and are probably far more common than has been recorded. The reported "freshwater" records include a mixture of terrestrial species that favour damp habitats and interloping marine/brackish species. It is well known that when freshwater planarians are absent from oceanic islands they may be "replaced" by marine taxa (Ball & Hay 1977).

At least four species of flatworm are known from Macquarie Island. Evans (1970) mentions several *en passant*. Ball & Hay (1977) described the endemic *Duplominona amnica* from streams and lakes. Winsor & Stevens (2005) describe *Arthurdendyus vegrandis* and confirm *Kontika andersoni* from damp habitats, while Dartnall *et al.* (2005) note a large unidentified species with an arrow-shaped head, two conspicuous eyespots and a broad diamond-shaped tail at one of Evans' sampling sites as well as confirming the widespread presence of *D. amnica*. *Arthurdendyus vegrandis* and *K. andersoni* which are *(sensu stricto)* terrestrial predators of earthworms normally occur in damp moss and under stones rather than truly immersed in streams. Therefore both are marked as interlopers in table 1. Both *Duplominona amnica* and the unidentified species of Dartnall *et al.* (2005) are freshwater species. The abundance and wide range of the marine *D. amnica* in the lakes of Macquarie Island was noted as "a surprise" to Ball & Hay (1977).

Points of interest (Platyhelminthes)

There are no parasitic flatworms reported from freshwater habitats in the Antarctic region.

Free-living flatworms are poorly known, warrant further study, and are widespread in Antarctic freshwaters.

Key references

MqI: Evans (1970), Ball & Hay (1977), Marchant & Lillywhite (1994), Dartnall *et al.* (2005), Winsor & Stevens (2005), Greenslade (2006). **HI**: Dartnall (1995a, 2003, 2006). **C**: Beauchamp (1939, 1940), Jeannel (1940), Davies & Young (1974). **PE**: Dartnall & Smith (2012). **SG**: Dartnall & Heywood (1980), Headland (1984, pers. comm.), Dartnall (2005c). **SO**: Heywood *et al.* (1979, 1980), Priddle & Dartnall (1978). **SS**: Simonov (1973). **Sch**: Ingole & Parulekar (1990, 1993). **PCM**: Dartnall (unpublished). **LH**: Dartnall (1995b). **VH**: Dartnall (2000). **McM**: Murray (1910a), Armitage & House (1962), Dougherty & Harris (1963), Bierle (1969), Webster-Brown *et al.* (2010).

Phylum Nemertea

No freshwater nemerteans have been reported from the Antarctic region.

Phylum Entoprocta

No freshwater entoprocts have been reported from the Antarctic region.

Phylum Rotifera

Fast breeding rates, the production of resting eggs and the ability to withstand dehydration and freezing means that some species of rotifer are ideally suited to life in the Antarctic (Dartnall 1992). With some 150 species so far known rotifers are easily the most numerous freshwater group present (table 1: Rotifera). Large though this number is, it is less than one quarter of the species currently known for the United Kingdom and less than one fifth of those known from Australia. Detailed studies have been carried out at several locations but there are considerable gaps. For example, from Crozet just four genera of rotifers (*Cephalodella, Lecane, Lepadella* and *Proales*) have been recorded, identified from the gut contents of the predatory freshwater amphipod *Pseudingolfiella possessionis* (De Smet 2015). Interestingly De Smet (2002a) recorded nine species from the littoral zones of both Îles Kerguelen and Crozet. This habitat is outside the scope of this paper but two of the species De Smet found (*Colurella colurus* and *Lindia torulosa*) are frequently found in freshwater and as such have been added to table 1 as interlopers. One of the others (*Proales reinhardti*), generally considered to be a marine species, has been reported from the ultra-freshwater Crooked Lake in the Vestfold Hills (Korotkevich 1958, Kutokova 1958b) and has similarly been included. However, it should be noted that Dartnall (2000) only found it at the eastern end of Ellis Fjord where the massive freshwater outflow from Lake Druzby flows into Ellis Fjord in the Vestfold Hills at a salinity of 22‰, suggesting a euryhaline and/or new species.

Until very recently the rotifers from the Antarctic region were thought to be benthic with just a few planktonic examples notably belonging to the genus *Notholca*. Different species of *Notholca* were noted across a range of locations (table 1: Rotifera: Brachionidae) variously characterised by striations, circular pits and the presence or absence of a tab on the posterior edge of the dorsal plate. Hannson *et al.* (2012) identified nine species of rotifer including seven planktonic species and a solitary copepod from samples taken at the ice-water interface and mid-water of Lake Hoare, a permanently ice-covered lake in one of the Dry Valleys of the McMurdo Sound region.

While a few rotifers – e.g., *Collotheca ornata cornuta, Epiphanes senta, Lepadella patella, Ptygura crystallina, Resticula gelida* – are truly cosmopolitan, the majority are restricted to the sub-Antarctic islands and maritime Antarctic. *Adineta grandis, Philodina alata, P. antarctica* and *P. gregaria* are endemic to Antarctica. Neither *A. grandis* nor *P. gregaria* have been found on the South Shetland islands, an archipelago apparently well within their range. The South Shetland islands have been subjected to numerous rotifer studies (de Paggi 1982, Kuczynski 1987, Janiec 1993, Janiec & Salwicka 1996, Downie *et al.* 2000, Toro *et al.* 2007, Nędzarek & Pociecha, 2010), but neither bdelloid has been reported from there; indeed Susanna de Paggi (pers. comm.) specifically looked for *Philodina gregaria* but did not find it.

The Digononta or Bdelloidea are poorly known (table 1: Rotifera: Bdelloidea) and are undoubtedly far more common than indicated. Recent molecular genetic studies have enabled Velasco-Castrillón *et al.* (2014) and Iakovenko *et al.* (2015) to identify a number of new species. Working with samples from Victoria Land (McMurdo Sound region) and from the South Shetland Islands and the northern tip of the Antarctic Peninsula Iakovenko *et al.* (2015), recognised 60 morphospecies. Twenty were only identified to the generic level and could not be attributed; no data were available for thirteen others that showed no discernible differences from known cosmopolitan species, while ten possessed minor differences from presumed cosmopolitan bdelloids. This left seventeen Antarctic

endemics, six of which were previously known, plus eleven new (described) species. Although Iakovenko *et al.* (2015) worked predominately with soil samples several of their species had been described as cosmopolitan freshwater inhabitants in earlier studies (Murray 1910b, Dougherty & Harris 1963, Donner 1972, Dartnall & Hollowday 1985). Thus species previously identified as *Adineta barbata, A. gracilis, Habrotrocha constricta, Macrotrachela insolata* have been renamed *A. coatsae, A. editae, H. antarctica* and *M. donneri* respectively. *Adineta* sp. A from Heard Island (Dartnall 1995a) becomes *A. emsliei* and *Philodina* sp. A from the South Orkney Islands (Priddle & Dartnall 1978, Dartnall & Hollowday 1985) is now *Philodina dartnallis* (Iakovenko *et al.* 2015). Confirmation of the identity of other sub-Antarctic bdelloid species will have to wait until they are clarified by molecular genetics.

Recently De Smet (2009) reported the first case of parasitism in Antarctic freshwaters; that of the rotifer *Pourriotia carcharodonta* parasitising the xanthophyte *Vaucheria geminata* (Vaucher) de Candolle by causing it to produce galls.

Points of interest (Rotifera)

Rotifers are found throughout the Antarctic region.

The endemic bdelloids *Philodina gregaria* and *Adineta grandis* have circumpolar distributions and are not found on the sub-Antarctic islands.

The endemic bdelloids *Philodina alata,* and *P. antarctica* have limited distribution in eastern Antarctica.

Clarification of the interrelationships and distributions of *Notholca* species is required.

Clarification of the various species of Brachionidae is required.

Key references

MqI: Dartnall (1990, 1993), Dartnall *et al.* (2005), Fontaneto *et al.* (2015). **HI**: Dartnall (1995a, 2003, 2006). **K**: Beauchamp (1940), Russell (1959), Lair & Koste (1984), De Smet (2001, 2003). **C**: De Smet (2015). **PE**: Dartnall & Smith (2012). **SG**: Dartnall & Heywood (1980), Dartnall & Hollowday (1985), Dartnall (2005a, 2005c). **SO**: Dartnall & Hollowday (1985). **SS**: de Paggi (1982), Kuczynski (1987), Janiec (1993), Janiec & Salwicka (1996), Downie *et al.* (2000), Toro *et al.* (2007), Nędzarek & Pociecha (2010). **AP**: Schmitt (1945), Heywood (1977b), Dartnall (1980), Kuczynski (1987). **Sch**: Ingole & Parulekar (1987), Kutikova (1991), Mitra (1999). **TH**: Opalinski (1972b), Sharov *et al.* (2015). **PCM**: Dartnall (unpublished). **LH**: Dartnall (1995b). **VH**: Korotkevich (1958), Kutikova (1958b), Everitt (1981), Dartnall (1997, 2000). **Has**: Opalinski (1972a), Donner (1972). **OH**: Korotkevich (1958), Kutikova (1958b). **BH**: Korotkevich (1958), Kutikova (1958a, 1958b), De Smet & Gibson (2008). **WL**: Thomas (1965, 1972), Dartnall (2005b). **McM**: Murray (1910b), Armitage & House (1962), Dougherty & Harris (1963), Donner (1972), Spurr (1975), Cathey *et al.* (1981), Suren (1990), Hansson *et al.* (2012). **General references**: Koste (1978), de Paggi & Koste (1984), Sudzuki (1988), Segers (2007), Fontaneto *et al.* (2015).

Phylum Micrognathozoa

Just one species of this rare recently-described group of aschelminthes-like animals akin to the Rotifera and Acanthocephala has been reported from the Antarctic region. De Smet (2002b) found *Limnognathia maerski* amongst submerged mosses in stagnant and running water on Îles Crozet (table 1: Micrognathozoa). The only other record of this species is from the Arctic at Disko Island, West Greenland (Kristensen & Funch 1995, 2000).

Phylum Gastrotricha

These small solitary worms are easily overlooked. There are few casual Antarctic records principally from the sub-Antarctic islands (table 1: Gastrotricha). Several genera have been variously identified according to the presence of "scales" (*Lepidodermella*) and "hairs or spines" (*Chaetonotus*) and their shape and size. Gastrotrichs were not observed during an extensive survey of the freshwater lakes of the Vestfold Hills (Dartnall 2000) nor from the nearby Larsemann Hills (Dartnall 1995b), but they have been noted elsewhere in continental Antarctica, including Coast Lake in the McMurdo Sound area (Murray 1910a, Bierle 1969) and from a moss water community at Langhovde near the Japanese Syowa Station (Sudzuki 1964), though this last report is a terrestrial record (table 1: Gastrotricha).

Points of interest (Gastrotricha)

Rarely reported, gastrotrichs are undoubtedly more widespread in the Antarctic region than current studies would indicate.

Key references

MqI: Dartnall *et al.* (2005). **HI**: Dartnall (1995a, 2003, 2006). **PE**: Dartnall & Smith (2012). **SG**: Dartnall & Heywood (1980), Dartnall (2005c). **SO**: Heywood *et al.* (1979), McInnes & Pugh (1999). **SS**: Downie *et al.* (2000). **McM**: Murray (1910a), Bierle (1969).

Phylum Acanthocephala

There are no freshwater Antarctic records for this parasitic group.

Phylum Nematoda

Nematodes are a ubiquitous group that include specialised feeders on bacteria, fungi and algae as well as omnivores and predators. They are unusual in that some species can tolerate anoxic conditions. In the freshwater ecosystems of the Antarctic region nematodes are poorly known, especially from the sub-Antarctic islands with many surveys only mentioning their presence (table 1: Nematoda). Improved sampling techniques that focus on benthic sediments should increase the tally.

In 1998 Andrássy reviewed the free-living nematodes of Antarctica, reporting distinct maritime Antarctic and continental Antarctic populations. Since then a considerable number of new, predominately terrestrial species have been added to this list (Boström 1997, 2005, Nędelchev & Peneva 2000, Downie *et al.* 2000, Sohlenius *et al.* 2004, Ghosh *et al.* 2005, Ryss *et al.* 2005, Andrássy & Gibson, 2007, Andrássy 2008, Bohra *et al.* 2010). The total number of named species of terrestrial, freshwater

and saline nematodes from the Antarctic region south of 60°S currently stands at 68. Some 34 of these are recorded from continental Antarctica and 37 from the maritime Antarctic with just three species common to both, thus corroborating Andrássy's two distinct Antarctic populations (Velasco-Castrillo *et al.* 2014). Currently the freshwater species of nematodes from the sub-Antarctic islands are too poorly known to contribute to this discussion.

The Schirmacher Oasis list of nematodes is composed of species collected in and around the lakes (Ingole & Parulekar 1987, Sanyal 2004, Bohra *et al.* 2010, Gantait & Chandra 2017 and others) from both shallow freshwater and terrestrial habitats. Collections from clearly terrestrial habitats (Bohra *et al.* 2010) have been excluded from this review, leaving the remainder whose precise habitats are unspecified but include soil samples as well as floating algae and submerged lake mosses (table 1: Nematoda).

From penguin rookery pools on Marion Island Dartnall & Smith (2012) recovered a small number of large nematodes each with an impressive buccal cavity comprising three double hooks. They considered these nematodes to be gut parasites of marine origin that had been voided from their penguin hosts. If this is the case no nematodes parasitic on freshwater animals or plants have been reported from the Antarctic region.

Points of interest (Nematoda)

An important freshwater group but poorly known due to the difficulties of sampling benthic habitats in deep water. More samples required especially from the sub-Antarctic islands.

Free-living freshwater nematodes occur throughout the region.

No parasitic species are reported from sub-Antarctic or Antarctic freshwaters.

The nematode faunas of continental Antarctica and the maritime Antarctic are markedly different. When more is known of the sub-Antarctic nematode fauna it will be interesting to see where its relationships lie.

Key references

MqI: Marchant & Lillywhite (1994), Nicholas & Marples (1995), Dartnall *et al.* (2005). **HI**: Dartnall (1995a, 2003, 2006), Maslen (pers. comm.). **C**: Kir'yanova (1964). **PE**: Dartnall & Smith (2012). **SG**: Dartnall & Heywood (1980), Dartnall (2005a). **SO**: Heywood *et al.* (1979), Dartnall (1992). **SS**: Maslen (1979), Janiec (1993), Downie *et al.* (2000), Toro *et al.* (2007), Nędzarek & Pociecha (2010). **AP**: de Man (1904), Heywood (1977b), Maslen (1982). **Sch**: Ingole & Parulekar (1990), Bohra *et al.* (2010), Gantait & Chandra (2017). **PCM**: Dartnall (unpublished). **LH**: Dartnall (1995b). **VH**: Everitt (1981), Dartnall (2000), Andrássy & Gibson (2007). **OH**: Korotkevich (1958). **BH**: Korotkevich (1958), Kir'yanova (1964), Maslen (pers. comm.). **McM**: Murray (1910a), Suren (1990), Webster-Brown *et al.* (2010).

Phylum Nematomorpha

No freshwater nematomorphs have been reported from the Antarctic region.

Phylum Mollusca

Terrestrial gastropods are known from a number of the sub-Antarctic islands (Pugh & Scott 2002) occuring in the vicinity of freshwater lakes and pools but they are not aquatic. While *Notodiscus hookeri* (Reeve, 1854) has been reported as a major food source of the trout (*Salmo trutta*) on Marion Island (Cooper *et al.* 1992), these snails never venture into the water but were plucked off the vegetation that overhung the stream into which these fishes had been introduced. Dartnall & Smith (2012) found the introduced slug, *Deroceras panormitanum* (Lessona & Pollonera, 1882), in some numbers in a mire and a lake on Marion Island following a heavy downpour and while they were alive at the time of collection the slugs did not survive immersion leading to the conclusion that they had been washed in. Shells of limpets and several inshore marine snails were occasionally seen in shallow water in freshwater lakes and pools on Macquarie Island and the South Orkney Islands (Dartnall unpublished) but again these are cases of accidental introduction, dropped by passing seabirds.

Points of interest (Mollusca)

No freshwater snails or bivalves have been recorded from the Antarctic region.

Phylum Annelida

The phylum Annelida comprises three classes – Polychaeta, Oligochaeta, and Hirudinea. Most polychaete worms are marine; a few freshwater species are known elsewhere but none has been reported in freshwater from the Antarctic region. Similarly leeches (Hirudinea) are not known from freshwater or indeed from terrestrial habitats in the Antarctic. This leaves only the oligochaetes to consider.

Representatives of six oligochaete families have been found in the region – the larger, predominantly terrestrial "earthworms" Acanthodrilidae and Lumbricidae; and the smaller, thinner, predominantly aquatic Tubificata families Enchytraeidae, Naididae, Phreodrilidae and Tubificidae.

The Acanthodrilidae is a small group of closely related southern hemisphere earthworms. The genus *Microscolex* is predominately terrestrial with different species occurring on many of the sub-Antarctic and cool-temperate islands. They usually occur in damp conditions amongst moss, in the soil and/or under stones. Kok (1977) reported *Microscolex kerguelensis*, a terrestrial species, previously known from Îles Kerguelen (Tétry 1947, Lee 1968, Sims 1971, Duchêne 1989), on Heard Island (Lee 1968), and in a number of the freshwater lakes on the east coast of Marion Island. It was not found by Dartnall & Smith (2012) in their survey of the freshwater lakes of Marion Island and has been recorded as a terrestrial interloper in table 1: Annelida: Acanthrodrilidae. Evans' (1970) record of *M. macquariensis* from Scoble Lake, a plateau lake some 200 m above sea level on Macquarie Island, is also considered to be a terrestrial interloper as neither Marchant & Lillywhite (1994) nor Dartnall *et al.* (2005) found it in their surveys of streams and lakes on Macquarie Island.

Two genera of Lumbricidae have been reported from the Antarctic region – *Dendrodrilus rubidus* and *Eiseniella tetraedra* (table 1: Annelida: Lumbricidae). *D. rubidus* is Holarctic and has been introduced to the southern hemisphere including the sub-Antarctic islands (Blakemore 2002, Greenslade 2006). It has been recovered from the freshwater lakes and streams on Heard Island (Dartnall 2003), while on Îles Kerguelen (Duchêne 1989), Îles Crozet (Frenot 1985) and Macquarie Island (Lee 1968) it occurs in damp terrestrial habitats (note that these terrestrial records are not included in table 1: Annelida: Lumbricidae while the Heard Island record is shown as an introduced species in the "wrong environment"). *E. tetraedra* is a semi-aquatic worm inhabiting wells, springs and underground waters elsewhere in the world. In the Antarctic region (table 1: Annelida: Lumbricidae) it has been recorded in freshwater at Îles Kerguelen (Lee 1968, Duchêne, 1989) where it is cited as an introduced species by Frenot *et al.* (2005). It has also been reported from Macquarie Island as a single specimen (Lee 1959). It has not been recorded subsequently suggesting it is no longer present (Greenslade 2006).

The four families that comprise the subclass Tubificata (table 1: Annelida: Tubificata) contain numerous freshwater inhabitants; most of the species from the Naididae, Phreodrilidae and Tubificidae are aquatic while the Enchytraeidae also include terrestrial and littoral examples.

In the Antarctic region two species from the family Naididae have been reported in freshwater – *Nais elinguis*, and a species of *Vejdovskyella*. *N. elinguis* is a cosmopolitan species that is very common in the streams on Macquarie Island (Marchant & Lillywhite 1994) and has also been found in freshwater on Îles Kerguelen (Tétry 1947). Dartnall & Smith (2012) reported *Vejdovskyella* amongst the algae in most of the lakes they sampled on Marion Island (table 1: Annelida: Naididae).

Three species of Phreodrilidae have been found in freshwater on the sub-Antarctic islands (table 1: Annelida: Phreodrilidae). Marchant & Lillywhite (1994) recorded an unidentified *Astacopsidrilis*, subsequently identified as *A. campbellianus* by Pinder & Brinkhurst (1997), from a number of streams on Macquarie Island while *Neodrillus crozetensis* and *N. kerguelensis* have been found amongst emergent plants in streams and in the run-off from bird colonies by the sea shore at a number of sub-Antarctic islands (table 1: Annelida: Phreodrilidae). Sludge worms (Tubificidae) can survive in heavily polluted conditions. Four species have been recorded in freshwater from the Antarctic region including endemic species on Macquarie Island and South Georgia (table 1: Annelida: Tubificidae).

Known as sewage worms or pot-worms, Enchytraeidae are often associated with dead and decaying material, many occupying the marine littoral zone below the high water mark. Only a few species have been found in freshwater including *Cognettia antipodum* from streams and algae above the high water mark on Macquarie Island (Benham 1922, Stephenson 1932) though it was not found by Marchant & Lillywhite (1994). The cosmopolitan white worm *Enchytraeus albidus* was found in freshwater, under stones and in shore collections on South Georgia (Stephenson 1932), but only in wet soil beside a stream on Kerguelen (Tétry 1947) and from rocks and crevices on Îles Crozet (Lee 1968). It is considered an introduced species on Macquarie Island where it has been found in the marine littoral and amongst the rotting timbers of a sealers hut (Benham 1905, Greenslade 2006).

Bona fide freshwater enchytraeids include *Cernosvitovia* sp. and *Mesenchytraeus* sp. from Macquarie Island (Marchant & Lillywhite 1994) plus a number of species of *Lumbricillus* (table 1: Annelida: Enchytraeidae). The latter includes *L. healyae* and *L.* sp. from freshwater streams on Livingstone Island (Rodriguez & Rico 2008), *L. incisus* from the nearby King George Island (Wang & Liang 1997), and an unidentified *Lumbricillus* sp. from a polluted pool on Marion Island (Dartnall & Smith 2012), possibly different from that found on Livingstone Island (Rodriguez & Rico 2008). *L. lineatus* has a wide ecological range and may occur in or near freshwater. It was regularly encountered by Marchant & Lillywhite (1994) during their survey of the streams on Macquarie Island but does not normally occur in freshwater (Greenslade 2006). Elsewhere it has been found amongst decomposing kelp on Macquarie Island (Lee 1968), Heard Island and Îles Kerguelen (Rota 2001) and from shore collections at Port Lockroy, Antarctic Peninsula, on the South Orkney Islands and on South Georgia (Stephenson 1932). *L. macquariensis* was found in freshwater streams on Macquarie Island (Benham 1905, 1915, 1922) but was not reported by Marchant & Lillywhite (1994). Elsewhere it has been found in damp soil at the edge of pools on Heard Island (Lee 1968) and from under stones at the edge of the beach on South Georgia (Stephenson 1932).

The kick-sampling techniques employed by Marchant & Lillywhite (1994) on Macquarie Island yielded six species of freshwater oligochaetes, considerably more than known from the other sub-Antarctic islands (table 1: Annelida). Employing this novel sampling method on other islands should yield many more freshwater oligochaetes with the cosmopolitan *Dendrodrilus rubidus*, *Nais elinguis*, and *L. lineatus* being likely candidates.

Finally an unidentified oligochaete worm has been reported from samples taken from in and around the periphery of the lakes and pools and swampy areas of the Schirmacher Oasis (Ingole & Parulekar 1987, 1993, Barman 2000). Ingole *et al.* (1987) found it in shallow water of Priyadarshini Lake. Not mentioned in subsequent reports (Mandal 2013, Gantait & Chandra 2017) the identity of this oligochaete and continuing presence wants verification.

Points of interest (Annelida)

Leeches and polychaete worms are not known from freshwater habitats in the Antarctic region.

Oligochaete worms from six families have been found in freshwater in the Antarctic region. Most are terrestrial or littoral species that favour damp conditions that may lead them occasionally to be found in freshwater.

Freshwater oligochaete worms have been found on the sub-Antarctic islands and at the northern end of the

Antarctic Peninsula but not from continental Antarctica (subject to the verification of the Schirmacher Oasis sighting).

The apparent abundance of tubifid worms on Macquarie Island is believed to be due to the kick-sampling techniques employed by Marchant & Lillywhite (1994) and when such techniques are employed on the other sub-Antarctic islands it is predicted that many more oligochaete worms will be found.

Key references

MqI: Michaelsen (1900), Benham (1905, 1915, 1922), Stephenson (1932), Jamieson (1968), Lee (1959, 1968), Evans (1970), Marchant & Lillywhite (1994), Pinder & Brinkhurst (1997), Erséus & Grimm (2002), Dartnall *et al.* (2005), Greenslade (2006). **HI**: Lee (1968), Dartnall (2003). **K**: Michaelsen (1902, 1905b, 1914), Černosvitov (1935), Tétry (1947), Lee (1968), Sims (1971), Duchêne (1989). **C**: Michaelsen (1905b, 1914), Tétry (1947). **PE**: Tétry (1947), Sims (1971), Kok (1977), Dartnall & Smith (2012). **SG**: Michaelsen (1888, 1905a, 1921), Stephenson (1932), Erséus & Grimm (2002). **SO**: Stephenson (1932), Block *et al.* (1984), Heywood (1987). **SS**: Brinkhurst & Marchese (1987), Wang & Liang (1997), Downie *et al.* (2000), Toro *et al.* (2007), Rodriguez & Rico (2008). **Sch**: Ingole & Parulekar (1987).

Phylum Tardigrada

Tardigrades are microscopic animals that use piercing mouthparts to extract the contents of plant and animal cells. Best known as inhabitants of lichens, liverworts and mosses (hence colloquial "moss piglets") they also occur in marine and freshwater habitats (hence also "water bears") amongst the benthic vegetation. Their ability to withstand adverse conditions such as dehydration and freezing makes them ideally suited to Antarctic conditions. The phylum comprises two major classes – Heterotardigrada and Eutardigrada (Anderson 2001). The Heterotardigrada are largely marine but include both armoured terrestrial and a few freshwater species characterised by a thick cuticle. Freshwater and terrestrial Eutardigrada have a thin cuticle. All 910 known terrestrial species inhabit a film of water surrounding soil samples or on the surface of plants, and while many of these are occasionally found in freshwater only 62 species from 13 genera are true freshwater inhabitants (Garey *et al.* 2008).

Tardigrades occur throughout the Antarctic region as documented by Richters (1908a, 1908b, 1908c, 1909), Jennings (1976a, 1976b), Dastych (1984), Miller & Heatwole (1995), Miller J. *et al.* (1988) and Miller W. *et al.* (1994). Terrestrial habitats are much easier to sample than benthic sediments at the bottom of lakes. A list of the species found in freshwaters of the Antarctic region is given in table 1: Tardigrada. Here the hydrophilic genera (*Acutuncus, Dactylobiotus, Diphascon* and *Isohypsibius*); are separated from lake margin interlopers (*Echiniscus, Macrobiotus* and *Milnesium*), those that favour wet habitats (*Echiniscus* and *Mopsechiniscus*) or damp conditions (*Hypsibius*). *Diphascon pingue, Hypsibius dujardini, Isohypsibius papillifer* and *Ramazzottius oberhaeuseri* are all probably species groups rather than the single species nominated (McInnes pers. comm.).

Points of interest (Tardigrada)

Tardigrades are present throughout the Antarctic region where they are an important component of the freshwater fauna.

They are poorly known, especially in freshwater, and require further taxonomic and ecological studies.

Key references

MqI: Dartnall *et al.* (2005). **HI**: Dartnall (1995a, 2003, 2006). **PE**: McInnes *et al.* (2001), Dartnall & Smith (2012). **SG**: Dartnall & Heywood (1980), McInnes & Pugh (1999), Dartnall (2005c). **SO**: McInnes & Ellis-Evans (1987), McInnes (1995). **SS**: Janiec (1993), Downie *et al.* (2000), Toro *et al.* (2007), Nędzarek & Pociecha (2010). **AP**: Heywood (1977b), McInnes (pers. comm.). **Sch**: Ingole & Parulekar (1987, 1990, 1993), Mitra (1999), Hazra & Mitra (2002), Sanyal (2004). **TH**: Sharov *et al.* (2015). **PCM**: McInnes (pers. comm.). **LH**: Dartnall (1995b). **VH**: Dartnall (2000). **WL**: Thomas (1965). **McM**: Murray (1910c), Dougherty & Harris (1963), Suren (1990), Webster-Brown *et al.* (2010).

Phylum Arthropoda

The phylum is divided into four subphyla – Myriapoda, Hexapoda, Crustacea and Chelicerata (Anderson 2001). The exclusively terrestrial Myriapoda (centipedes and millipedes) are not considered further in this review. Some of the largely terrestrial Hexapoda have aquatic larvae. The Crustacea (crabs, shrimps and their kin) include numerous freshwater species while the Chelicerata (scorpions, spiders, ticks and mites) are predominantly terrestrial.

Hexapoda: comprises three classes – Ellipura, Diplura and Insecta. Neither the Ellipura nor Diplura are aquatic. Springtails (Ellipura: Collembola) have been noted in a number of freshwater surveys at Heard Island (Dartnall 1995a, 2003, 2006), South Georgia (Dartnall 2005c), Macquarie Island (Dartnall *et al.* 2005) and Marion Island (Dartnall & Smith 2012), but in every instance they were simply using the water surface as a substrate and so have been excluded from this review.

None of the following insects (Insecta) that have aquatic larvae – mayflies (Ephemeroptera), dragonflies and damsel flies (Odonata), stone flies (Plecoptera), water striders (Hemiptera), dobson and alder flies (Megaloptera), scorpion flies (Mecoptera) or caddis flies (Trichoptera) – have been found anywhere in the Antarctic region. This leaves just the beetles (Coleoptera) and true flies (Diptera) to consider. Only one species of aquatic beetle is known from the Antarctic region, the diving beetle *Lancetes angusticollis* from South Georgia (table 1: Arthropoda: Coleoptera).

A number of Diptera – midges, kelp flies, beach flies, crane flies, fungal flies, moth flies, etc – have been recorded from the sub-Antarctic islands and the northern tip of the Antarctic Peninsula. Many of these have moisture-loving larvae that commonly occur at low altitudes in swampy areas, amongst decaying kelp and vegetation or in mud, often close to the shore, alongside streams, in wallows

and brackish pools, and include a number of introduced species. As such they have occasionally been reported in freshwater though they are clearly brackish (littoral) or terrestrial interlopers.

Kelp flies occur around rotting beached kelp on the seashore. Marchant & Lillywhite (1994) recorded the larvae of both *Schoenophilus pedestris* and *Ephydrella macquariensis* in a number of the streams they sampled on Macquarie Island. They also found the crane fly *Erioptera pilipes* (= *Trimica pilipes*), but failed to secure larvae of the three species of moth flies – *Psychoda alternata* Say, 1824, *P. parthenogenetica* Tonnoir, 1940 and *P. surcoufi* Tonnior, 1922 – known from mud and wet earth on Macquarie Island (Greenslade 2006).

Midges (chironomid larvae) are restricted to moist environments (table 1: Arthropoda: Diptera), cannot survive even brief periods of desiccation (Ring *et al.* 1990) and occur in damp moss and peat, freshwater and brackish pools. *Eretmoptera murphyi* Schaeffer, 1914 has terrestrial larvae that live in damp moss and peat while *Belgica antarctica* Jacobs, 1900, *Listriomastax litorea* Enderlein, 1909, *Telmatogeton amphibious* (Eaton, 1875) and *T. macquariensis* (Brundin, 1962) and other *Halirytus* spp. inhabit brackish water at low tide on rocks and in pools above the high tide mark and in amongst algal debris. The larvae of any of these species may occur in coastal freshwater streams and lake edges as accidental contaminants. To date only the larvae of two introduced species *Limnophyes pusillus* and *Parochlus steinenii* have been found in freshwater (table 1: Arthropoda: Insecta: Diptera). *Parochlus steinenii* is reported from South Georgia (Brundin 1970) and the South Shetland Islands (Edwards & Usher 1985, Toro *et al.* 2007) where it has survived since being introduced from the Falkland Islands. A sibling species *Parochlus crozetensis* has been described from Îles Crozet (Serra-Tosio 1986). *Limnophyes pusillus* was probably introduced from Europe to the sub-Antarctic where it has successfully colonised freshwater habitats on Marion Island (Crafford 1986) and wet areas on Îles Kerguelen (Delettre & Tréhen 1977) (table 1: Arthropoda: Insecta: Diptera), while an unidentified species of *Limnophyes* has been reported from South Georgia (Brundin 1970). Two species of chironomid midge *Smittia* sp. and *Telmatogeton macquariensis* (Brundin, 1962) are known from Macquarie Island (Greenslade 2006). While larvae of neither species have been reported from freshwater their ecdysed larval cases were recovered from "the soak" at the northern end of Macquarie Island during the rotifer survey (Dartnall *et al.* 2005), suggesting they are blown in. Various species of *Telmatogeton* are known from many of the Southern Ocean islands, indeed Delettre *et al.* (2003) collected the larvae and pupae of an unidentified *Telmatogeton* sp. from mid-littoral epilithic algae at Spit Bay and Atlas Cove on Heard Island. They have not been found in freshwater and are not included. Similarly the midge *Forcipemyia* (*sic*) sp. (= *Forcipomyia*)is not included in table 1; apparently a single specimen was extracted using a Tullgren funnel from a moss sample from the Schirmacher Oasis (Sanyal 2004), here deemed to be terrestrial.

Points of interest (Hexapoda)

Just one species of diving beetle is known from the sub-Antarctic island of South Georgia.

Insects with moisture-loving larvae have been reported from the sub-Antarctic Islands and northern tip of the Antarctic Peninsula but very few have been reported from freshwater.

No insects have been reported from freshwater on the Antarctic continent if the midge *Forcipomyia* sp. from the Schirmacher Oasis is terrestrial.

Key references

MqI: Alexander (1962), Marchant & Lillywhite (1994). **K**: Delettre & Tréhen (1977). **C**: Serra-Tosio (1986). **PE**: Crafford (1986). **SG**: Brundin (1970), Nicolai & Droste (1984), Arnold & Convey (1998), Dartnall (2005c). **SO**: Block *et al.* (1984). **SS**: Edwards & Usher (1985), Toro *et al.* (2007). **Sch**: Sanyal (2004).

Crustacea: These are, when present the most obvious, diverse and well-documented of the Antarctic freshwater invertebrates. All eight major orders are represented (table1: Arthropoda: Crustacea) but with only a few records of Amphipoda and Isopoda (table 1: Arthropoda: Crustacea: Amphipoda and Isopoda). While crustaceans occur in all types of lake, there is a marked species decline with increasing latitude. The freshwater species of continental Antarctica are of particular interest being diverse and fragmented (table 1: Arthropoda). In 1994 Bayly found *Gladioferens antarcticus* alongside *Diacyclops mirnyi* in White Smoke Lake, a freshwater lake in the Bunger Hills. This lake is tidal, connected to the sea, but freshwater from top to bottom and therefore cannot be classified as a typical epishelf lake. *G. antarcticus* is believed to occur in greatest abundance close to the bottom at 90 m. *D. mirnyi* was originally described from a freshwater lake in the Bunger Hills (Borutzky & Vinogradov 1957), confirmed by Borutsky (1962) and Brodsky & Zvereva (1976), and subsequently reported from the Vestfold Hills in the ultra freshwater Lake Krutvatnet (Crooked Lake) and Lebed' Lake, which has a salinity 6.5 times higher than sea water (Korokevich 1958, Borutsky 1962), though the latter record is due to contamination. Dartnall (2000) did not find it on two visits to Lebed' Lake but found it in eight large freshwater lakes and six smaller fresh/slightly brackish lakes in the Vestfold Hills. Dartnall (1995b) also reported it from a number of freshwater lakes in the Larsemann Hills. Dartnall & Hollwedel (2007) ascribed this species to the smaller *Diacyclops* they found in the Falkland Islands, but acknowledged the species is inadequately described and in need of revision. More recently Karanovic *et al.* (2013) examined cyclopoid copepods from three ice covered lakes on Continental Antarctica and erected three new species – *Diacyclops kaupi* from the epishelf Transkriptsii Gulf, Bunger Hills, *D. walkeri* from epishelf Pineapple Lake, Vestfold Hills, and *D. joycei* from proglacial Lake Joyce, McMurdo Sound Dry Valleys. With the loss of the *D. mirnyi* type specimens new material is required to elucidate the status of all these records.

Other crustaceans with interesting distributions include *Boeckella poppei* from South Georgia, the South Orkney Islands, South Shetland Islands and on the Antarctic Peninsula (Pugh *et al.* 2002). These records should be coupled with Bayly & Burton's 1993 report of dwarf specimens from Beaver Lake, Prince Charles Mountains along with the juvenile *Boeckella* sp. from Lake Hoare (Hansson *et al.* 2012) (table 1: Arthropoda: Crustacea: Calanoida) and the exceptionally variable specimens reported from the Falkland Islands (Dartnall & Hollwedel 2007). The unusual Continental Antarctic and sub-Antarctic distribution of *Daphniopsis studeri* also requires further investigation (table 1: Arthropoda: Crustacea: Cladocera).

The benthic dwelling harpacticoid copepods are primarily confined to the sub-Antarctic islands. The two ecdysed skins of a small harpacticoid, a member of the family Canthocamptidae, were recoverd from deep in Blue Lake on Ross Island (Murray 1910a) and are believed to have been blown in as they have not been recorded since. *Zaus contactus* is believed to be a mistaken identification according to Pugh *et al.* (2002) since it has not been reported from Macquarie Island for more than 100 years (Chilton 1909, Smith & Sayers 1971). Pugh *et al.* (2002) think that *Bryocamptus zschokkei* likely refers to *Antarctobiotus robustus*. *Tigriopus angulatus* occurs in brackish pools on coastal terraces while *Epactophanes richardi* and *Marionobiotus jeanneli* are common in freshwater streams and pools.

Ostracods are not known from the Antarctic continent, but have been reported from the South Orkney Islands and most sub-Antarctic islands. Their apparent absence from Heard Island is surprising; it is not yet clear whether this is a true observation or a sampling omission (table 1: Arthropoda: Ostracoda).

There are records of only three amphipods from the region (table 1: Arthropoda: Crustacea: Amphipoda). Both the unidentified amphipod on South Georgia (Weller 1975) and *Kergueleniola macra*, known only as a single specimen from the gut of the introduced brook trout (*Salvelinus fontinalis*), on Îles Kerguelen (Ruffo 1970) need confirmation (Pugh *et al.* 2002). Recently, De Smet (2015) described a new species, *Pseudingolfiella possessionis*, from streams on the Crozet Archipelago (table 1: Arthropoda: Crustacea: Amphipoda).

The unidentified *Iais* species found at Macquarie Island (Evans 1970) belongs to a large family of predominantly marine isopods (Wilson & Wägele 1994). The genus is usually ecto-commensal on marine isopods, though free-living freshwater species have been found on Amsterdam (Chappuis 1958) and Gough (Holdgate 1961) islands suggesting the genus may have (repeatedly) invaded freshwater on Macquarie and other remote islands. Evans' (1970) Macquarie Island specimens were only found in freshwater streams, the habitat subsequently confirmed by Marchant & Lillywhite (1994). Wilson & Wägele (1994) suggested the specimens occurring interstitially at sea level in brackish pools and in freshwater streams on Macquarie Island actually comprise three unidentified species.

The distributions of the various freshwater crustaceans shown in table 1: Arthropoda: Crustacea are largely uncontentious. *Pleuroxus truncatus* was recorded by Pesta (1928) from freshwater lakes on South Georgia but has not been reported since, suggesting it is a possible misidentification or an ephemeral introduction (Pugh *et al.* 2002).

Points of interest (Arthropoda: Crustacea)

Both the anostracan *Branchinecta gaini* and the anomopodan *Macrothrix oviformis* are restricted to the islands of the Scotia arc.

Ovalona weinecki is known from the South Orkney, South Shetland and sub-Antarctic islands.

Daphniopsis studeri has a very unusual and wisespread distribution. It has been found on the sub-Antarctic islands of Heard, Kerguelen, Crozet and Marion, and on the Antarctic continent immediately to the south of these islands at the Colbeck Archipelago, and in the Larsemann and Vestfold Hills.

Various ostracods are restricted to the South Orkney and sub-Antarctic islands.

The distribution and taxonomy of the calanoid copepod *Boeckella* spp., and of the cyclopoid copepod *Diacyclops* spp. warrant further study.

Freshwater harpacticoid copepods are restricted to the sub-Antarctic islands.

Amphipods and isopods are poorly known and represented in the Antarctic region.

Key references

MqI: Evans (1970), Tyler (1978), Dartnall (1993), Marchant & Lillywhite (1994), Dartnall *et al.* (2005). **HI**: Bayly (1992), Dartnall (1995a). **K**: Brady (1875, 1879), Eaton (1876), Studer (1878), Brehm (1954), Dreux (1970), Ruffo (1970), Gay (1981, 1982). **C**: Dreux (1970), De Smet (2015). **PE**: Kiefer (1944), Kok & Grobbelaar (1978), Dartnall & Smith (2012). **SG**: Mrázek (1892), Poppe & Mrázek (1894), Ekman (1905), Pesta (1928), Harding (1941), Heywood (1970a), Weller (1975), Weller (1977), Dartnall & Heywood (1980), Hessen *et al.* (1989), Dartnall (2005c). **SO**: Harding (1941), Heywood (1967, 1970a, 1970b, 1977a), Weller (1977), Clarke *et al.* (1989), Ellis-Evans & Walton (1990). **SS**: Campos *et al.* (1978), Jurasz *et al.* (1983), Janiec (1993), Paggi (1983, 1987, 1996), Toro *et al.* (2007), Pociecha (2007), Nędzarek & Pociecha (2010). **AP**: Bryant (1945), Schmitt (1945), Heywood (1977b), Dartnall (1980). **TH**: Sharov *et al.* (2015). **PCM**: Bayly & Burton (1993). **LH**: Dartnall (1995b). **VH**: Borutzky (1962), Dartnall (2000), Karanovic *et al.* (2013). **BH**: Borutzky & Vinogradov (1957), Bayly (1994), Bayly *et al.* (2003), Karanovic *et al.* (2013). **McM**: Murray (1910a), Hansson *et al.* (2012), Karanovic *et al.* (2013). **General References**: Lofthouse (1967), Smith & Sayers (1971), Frey (1987, 1988, 1993), Kotov (2007).

Chelicerata: Few of the *circa* 400 free-living and largely terrestrial and marine mites reported from the Antarctic region (Pugh 1993) have been recorded from freshwater. Pugh & Dartnall (1994) concluded that most mites collected from streams, lakes and brackish pools of the

region were either terrestrial species blown in by the wind or interlopers from the littoral environment that had invaded coastal brackish pools. This tenet has been endorsed by subsequent studies on the sub-Antarctic islands Macquarie (Dartnall *et al.* 2005), Heard (Dartnall 2006), Prince Edward (Dartnall & Smith 2012) and South Georgia (Dartnall 2005c). There are no bona fide records of freshwater mites on the Antarctic continent (table 1: Arthrodopa: Arachnida: Acarida).

Those species noted from freshwater but usually associated with the marine littoral zone include the genera *Gamasellus* (Rhodacaridae: Mesostigmata), *Alaskozetes*, *Antarcticola* and *Halozetes* (Podocaridae: Cryptostigmata), *Hyadesia* and *Neohyadesia* (Hyadesiidae: Astigmata) (Hughes & Goodman 1969, Lee 1970, Fain 1975, Schenker 1986, Luxton 1990, Pugh 1993). Note that *Antarcticola georgiae* Wallwork, 1970 (Cryptostigmata) and *Hyadesia halophila* Fain, 1975 (Astigmata), both of which were collected on South Georgia (Dartnall 2005c) have not been included in this survey as they were only found in brackish pools outside the freshwater limits of this analysis.

The remaining mites – *Bryobia practiosa*, a *Tetranynchus* sp. (Prostigmata); *Globoppia intermedia longiseta*, *Halozetes belgica*, *Magellozetes antarcticus*, *Platynothrus skottsbergii*, *Trimalaconothrus flagelliformis*, and an unknown larva, all Cryptostigmata listed in the Pugh & Dartnall 1994 survey, together with two oribatid mites, *Edwardzetas elongatus* and *Trimaloconothrus flagelliformis*, subsequently recorded by Pugh (1996) – are terrestrial species that were accidentally washed or blown into freshwater. Of these *Bryobia pratiosa* and *Tetranychus* sp. (Tetranychidae: Prostigmata) together with the two unidentified Acaridae (Astigmata) are probably non-indigenous aliens (Pugh 1993, 1994). *Algophagus antarcticus* (Hyadesiidae: Astigmata) from Heard Island (Pugh & Dartnall 1994) is probably a bona fide aquatic mite having been recorded from numerous brackish and freshwater pools close to the shore (Hughes 1955, Pugh & Dartnall 1994), but this species has also been recorded from amongst vegetation and humus (Fain 1975), which makes its exact status uncertain. The unknown species of *Glycyphagus*, recorded from Heard Island (Dartnall 2006) is now believed to be an accidental contaminant and has been eliminated from this survey.

The 16+ species of mite reported from the Schirmacher Oasis (Barman 2000, Sanyal 2004, Gantait & Chandra 2017) are similarly either terrestrial species blown in by the wind or interlopers from the littoral environment. These samples were obtained with a small hand-held scoop from floating algae, submerged mosses and soil samples collected in and around the peripheries of the lakes (table 1: Arthropoda: Arachnida) – a mixture of terrestrial and very shallow water habitats. These mites, none of which appears to be true freshwater inhabitants include a puzzling mix of mites that are elsewhere found as pests of stored food, inhabitants of bird's nests and on rocks and lichens.

The three specimens of the spider (*Myro kerguelensis* Pickard-Cambridge, 1876) found in the preserved samples from Scholes Lagoon on Heard Island are terrestrial interlopers that have undoubtedly been washed or blown into that lake (Dartnall 2006) as is the single specimen of *Prinerigone vagans* Andouin,1826 from Marion Island (Dartnall & Smith 2012). Whereas some terrestrial mites can withstand prolonged immersion in freshwater the life expectancy of these submerged spiders was short and consequently they have not been included in this survey.

Points of interest (Chelicerata)

Mites found in freshwater habitats on the sub-Antarctic islands and on the Antarctic Peninsula are predominantly littoral species that have invaded the near-shore brackish pools, or terrestrial species that have been washed or blown into the lakes and pools.

There are no records of aquatic spiders from the Antarctic region.

Key references

MqI: Pugh & Dartnall (1994), Dartnall *et al.* (2005). **HI**: Pugh & Dartnall (1994), Dartnall (2006). **PE**: van Pletzen & Kok (1971), Marshall *et al.* (1999), Bartsch (1999), Marshall *et al.* (2003), Dartnall & Smith (2012). **SG**: Pugh & Dartnall (1994), Dartnall (2005c). **SO**: Goodman (1969), Dartnall (1992), Pugh & Dartnall (1994). **SS**: Trägårdh (1907). **AP**: Ewing (1945). **Sch**: Ingole & Parulekar (1987, 1990, 1993), Barman (2000), Sanyal (2004), Gantait & Chandra (2017). **General reference**: Pugh (1993).

Phylum Ectoprocta

No freshwater ectoprocts have been reported for the Antarctic region.

Phylum Vertebrata

Most of the vertebrates found in the Antarctic region are marine and fall outside the scope of this study. There are no native Antarctic freshwater fishes, though a number of salmonid fishes have been introduced into sub-Antarctic lakes and a couple of inshore benthic fishes are reported from epishelf lakes. The reports of fish scales from the benthic sediments of freshwater lakes in the Vestfold Hills (Dartnall 2000) are by-product of seabird (skua and/or gull) regurgitations and/or droppings. There are two recorded incidents of fishes being caught in epishelf lakes. Heywood & Light (1975) caught four specimens of the emerald rockcod (*Trematomus bernacchii* Boulenger, 1902) in a fish trap lowered down to 70 m into 117 m-deep Ablation Lake, Alexander Island. Here seawater (salinity of 32‰) occurs below 66.5 m; the top 53 m are fresh (0.1–1‰) with a steep halocline between 66 m and 66.25 m where the salinity increases from 18–31.5‰. These fish were presumed to have been caught on the bottom, below this depth, rather than while the fish trap was being lowered or raised as they exhibited signs of acute distress on being hauled up to the surface (Heywood 1977b). The fact that their stomachs were full of recently ingested marine fish and invertebrates (Heywood 1977b) confirms their seawater habitat and would appear to deny any adaption to freshwater. Cromer *et al.* (2005) caught a single specimen of the Crowned Rockcod (*Trematomus scotti* (Boulenger, 1907)) from Beaver Lake more than 100 km from the open sea. The fish was from the brackish-water zone of this epishelf lake and while it

did not appear to have suffered any ill-effects from being hauled up to the surface it is a common inshore marine fish, and, like the Emerald Rockcod, it is deemed to fall outside the scope of this survey.

A number of attempts were made to introduce salmon and trout into the lakes and streams of several sub-Antarctic islands with various degrees of success during the second half of the twentieth century (table 1: Chordata: Osteichthyes: Salmonidae). Brown Trout (*Salmo trutta*) and Brook Trout (*Salvelinus fontinalis*) were introduced at Îles Crozet and Marion Island (Prince Edward Islands). The Brown Trout survived on Marion Island for at least 20 years but the impoverished nature of the local habitat led to dwarfing of the resident population and those fish that successfully migrated to sea were unable to re-enter their home stream up a waterfall and eventually died out (Cooper *et al.* 1992). The Brook Trout on Marion Island have died out as the small lake they were released into has now become completely overgrown. Both species introduced to Crozet (table 1: Chordata: Osteichthyes: Salmonidae) are believed to be thriving (Frenot, pers. comm.). The experiment at South Georgia was "preliminary" with only ten Rainbow Trout (*Oncorhynchus mykiss*) introduced into Gull Lake in 1964 (Headland 1984). None has been seen since and the species is believed to have died out there.

A concerted and long-term program of fish introductions (1958–1990) was carried out at Îles Kerguelen in an attempt to establish a fishing industry. In some cases these introductions have proved viable though uneconomic. Of the eight alien species that have been introduced, the Lake Trout (*Salvelinus namaycrush*), Rainbow Trout (*Oncorhynchus mykiss*) and Chinook Salmon (*Oncorhynchus tshawytscha*) are now extirpated, and the Atlantic Salmon (*Salmo salar*) is becoming rare and will probably die out in the near future (table 1 Chordata: Osteichthyes). The Brown Trout (*Salmo trutta*), Brook Trout (*Salvelinus fontinalis*) and Coho Salmon (*Oncorhynchus kisutch*) are all breeding well while the Arctic Char (*Salvelinus alpinus)* is proving to be a very invasive alien (Davaine *et al.*1997, Frenot *et al.* 2005, Frenot pers. comm.) (table 1: Chordata: Osteichthyes).

No amphibians or reptiles have been found in the Antarctic region.

There are just five species of water fowl that are legitimate freshwater inhabitants of the sub-Antarctic islands (table 1: Chordata: Aves). Most of the birds found in the Antarctic region are marine and therefore not considered part of this survey. However, they all come ashore to breed and effluent run off from penguin breeding colonies into nearby lakes and pools has a marked effect on the water chemistry, dramatically affecting the flora and fauna.

Similarly, there are no freshwater mammals anywhere in the Antarctic region though when present elephant seals and fur seals can not only affect the topography of pools and wallows sites but radically alter the water chemistry of nearby water bodies with their effluent.

Points of interest (Vertebrata)

The only vertebrates occurring in freshwater in the Antarctic region are eight species of salmonid fishes that have been introduced into the sub-Antarctic islands, plus a few native and introduced waterfowl on the sub-Antarctic islands.

There are no native freshwater fish, amphibians, reptiles or mammals known from the Antarctic.

Seal wallows and the run-off from penguin breeding colonies can dramatically alter adjacent lakes and pool water chemistry and affect the flora and fauna.

Key references (fishes)

K: Lesel *et al.* (1971, 1972), Davaine & Beall (1982), Davaine *et al.* (1997), Duchêne (1989), Frenot *et al.* (2005). **C**: Watkins & Cooper (1986). **PE**: Cooper *et al.* (1992), Dartnall & Smith (2012). **SG**: Headland (1984).
Key references (aquatic birds): **MqI**: Frenot *et al.* (2005).
General references: Watson (1975).

DISCUSSION

This paper collates published information on the Antarctic freshwater fauna. Not everyone will agree with the definitions and limitations I have imposed in the introduction and indeed many elements of the fauna sit astride more than one category. Ideally one would like to compare like with like, using similar sampling equipment in a similar way at each location but the range of different water body types – streams, pools, lakes, epishelf lakes, etc – makes this impossible even before one considers confounding geographic and climatic differences. Even when one has seemingly similar locations varying sampling techniques can influence the results and live samples are invariably more productive in terms of numbers of species found than preserved samples.

Limnological studies in the Schirmacher Oasis have taken a different approach from those at other Antarctic sites. Here, concentration has been on hand corer and scoop samples of soil and moss turfs in and around the periphery of lakes, in marked contrast to net, deepwater and benthic samples widely used in studies elsewhere. Ingole & Parulekar (1987, 1990, 1993) sampled a number of lakes in the Schirmacher Oases and recorded protozoan species, two species of turbellarian, one species of rotifer, two species of nematode, two of tardigrade, an oligochaete and a springtail. They also reported that the maximum faunal density occurred in moss turf samples (Ingole & Parulekar 1987). Subsequent studies in the Schirmacher Oasis have focused on these moss turves enabling Gantait & Chandra (2017) to compile a faunal list of 17 species of protozoa, one species of rotifer, two species of tardigrade, 16 species of nematode, 16 species of mite, five of springtail and a midge for the area. From the descriptions of how these samples were collected and processed it is possible to conclude that many were taken alongside the lakes rather than from the water. Even after excluding the obviously terrestrial records the faunistic record of the area remains terrestrial in nature with little in common with the other oases.

From the information assembled it is clear that there are still gaps in our knowledge. Most freshwater samples have been collected from rock-bound lakes and pools

close to expedition bases. These freshwater habitats are typically oligotrophic though some are enriched with the run-off from nearby penguin rookeries and/or seal wallows. The fauna is predominately benthic in habitat and generally becomes more depauperate with increasing latitude (Dartnall & Heywood 1980). Planktonic species are rare and in some instances are suspected of being contaminants (Fontaneto *et al.* 2015). Only one case of parasitism has so far been identified.

The Antarctic continent's ice-covered centre, the continent's coastal fringe, the Antarctic Peninsula and sub-Antarctic islands that constitute the Antarctic region have a diverse range of water bodies to engage the limnologist. The presentation of the results as a continuum of slowly increasing latitude (table1) rather than as a set of segments divided by longitude segments keeps the various regions – sub-Antarctic, maritime Antarctic and continental Antarctic – together. From the table it is clear that, for example, the freshwater fauna of Macquarie Island has far more in common with that of South Georgia at comparable latitude than with that of McMurdo Sound, at comparable longitude and considerably closer (fig. 1).

Sub-Antarctic islands

On the sub-Antarctic islands lakes, rivers and pools are small and shallow and support similar floras and faunas. Terrestrial vegetation encroaches most of these water bodies so that it is sometimes difficult to identify the water/ dry land boundary resulting in some terrestrial species being found in the "wrong" environment. During the winter a thin film of ice may form on the surface of some of these water bodies but not even the shallowest freeze solid. None of these sub-Antarctic water bodies are brackish or saline with the exception of those in close proximity to the sea that are periodically inundated.

Volcanically-heated ground is known to exist, for example on Îles Kerguelen, but no heated water bodies from there have been sampled thus far.

Antarctic Peninsula

On the Antarctic Peninsula lakes, rivers and pools are again generally small and shallow. The water is generally oligotrophic though nearby seal wallows and/or the run off from penguin rookeries may turn some eutrophic. Lake edges are usually clearly defined with limited surrounding terrestrial vegetation and consequently limited contamination by terrestrial interlopers. During the winter the shallowest water bodies freeze solid and remain frozen for the winter months. These pools have a distinct summer fauna (tardigrades, nematodes and rotifers notably *Philodina gregaria*, *Adineta grandis*, *Epiphanes senta* but no crustaceans). The surface waters of larger water bodies freeze to a depth of approximately two metres and remain frozen for 8–10 months of the year.

Volcanically heated ground is known to exist, for example at Deception Island, and unidentified nematodes are particularly abundant in Kroner Lake (Downie *et al.* 2000) but no further details are available. As this lake is directly linked to the sea via a breached dam, it is classified as brackish and outside the scope of this paper. The faunas of the freshwater portions of epishelf lakes have remarkably few species. Even so epishelf lakes are considered by many to act as refugia – reservoirs of species for recolonisation following glacial maxima (De Smet & Gibson 2008).

Antarctic coastal fringe

On the Antarctic coastal fringe areas known as oases have brackish, saline and supersaline bodies of water that fall outside the scope of this review, as well as numerous freshwater lakes, rivers and pools dotted around the coast (fig. 1). Here the freshwater lakes may be considerably larger than those on the sub-Antarctic islands and on the Antarctic Peninsula. Again they are oligotrophic, with clearly defined lake edges, very limited surrounding terrestrial vegetation (the occasional moss bank), so that there is very little contamination by terrestrial invertebrate species.

During the winter the shallowest water bodies freeze solid and these pools have a distinct and limited summer fauna; rotifers, nematodes and tardigrades are present but no crustaceans. Small, shallow lakes that do not quite freeze solid become anoxic and are principally populated by nematodes during the summer open water period. The surface waters of the large southerly lakes may remain permanently ice-covered. These lakes have only recently been sampled and in several instances have yielded unexpected results. The planktonic rotifers reported from the Dry Valleys (Hansson *et al.* 2012) are presumably feeding on the diatom bloom found on the under surface of the ice of Lake Hoare.

Volcanically-heated ground is known to exist high up on Mt Erebus and Mt Terror on Ross Island and also on Mt Melbourne and Mt Rittman in Northern Victoria Land, but water bodies in these areas are currently unknown.

Epishelf lakes around the Antarctic continent are coastal and, like those on the Antarctic Peninsula, are depauperate. Cryoconite holes and proglacial lakes occur on and adjacent to glaciers. These water bodies are invariably ultra-oligotrophic and seemingly devoid of metazoans though they have been little sampled. Recently, however, Porazinska *et al.* (2004) reported two species of rotifer from cryoconite holes in glaciers in Victoria Land – *Philodina gregaria* which is normally found in eutrophic pools and *Cephalodella catellina* normally found in freshwater/ brackish pools.

Continental Antarctica

Finally, the Continental Antarctic ice cap covers at least 379 (often very large) subglacial lakes sitting on underlying bedrock, under thousands of metres of ice (Laybourn-Parry & Wadham 2014). Lake Vostok, the largest of these, is ca. 250 km long, 50 km wide and under 4 km of ice. Media reports of bacteria in this lake, when it was sampled in 2013, have yet to be confirmed and may turn out to be contaminants rather than endemics. Supraglacial lakes

formed from meltwater on the surface of the ice cap are unlikely to have much of a flora and fauna.

Various hypotheses have been put forward to explain the distributions of invertebrates in the Antarctic region, including colonisation via land bridges, continental drift, airborne, animal-mediated, and anthropogenic introductions, and relict (cryoconite/epishelf lake) faunas, but no single explanation fits all. Colonisation should be seen as an ongoing process by a continual stream of potentially invasive plants and animals. Most are transient and fail to establish breeding populations. The sub-Antarctic islands surrounded by vast inhospitable seas represent a very small target for any potential freshwater invader and whilst the Antarctic continent represents a much bigger target, suitable freshwater habitats are more remote, rare and tiny. The wealth of species present in the Antarctic region as a whole is a tribute to the tenacity of nature. Global climate change offers already established species the opportunity of extending their range and increases the likelihood of new species gaining a foothold. Recently a number of non-native or alien species – midges and mosquitos – have been reported. Chironomids are thought to have been introduced to the Scotia arc islands during the 1960s (see Hexapoda above). Black fungus midges, mushroom gnats and mosquitos have been noted at several Antarctic research stations (Hughes *et al.* 2005, Peter *et al.* 2013), but have not been included in this survey as they are confined within sewage treatment plants and other station buildings (Hughes *et al.* 2015). They are either not believed to constitute an invasive threat (Peter *et al.* 2013), or have already been eradicated (Convey *et al.* 2006).

As early scientists were armed with European keys (usually the only ones available) it is not surprising that many northern hemisphere species have been recorded from the Antarctic region thereby reinforcing the then long-held belief in the ubiquitous nature of the fauna. While some species are truly cosmopolitan, notably amongst the pliomate rotifers, modern improvements and modifications in taxonomy mean that some earlier identifications are now being challenged and old mistakes corrected.

Boeckella poppei (Calanoida: Arthropoda), for example, was erroneously identified as *Pseudoboeckella silvestrii* by Harding in 1941, a noted copepod expert of his time, and was not corrected until 1977 (Heywood 1977a). In 1957 Borutzky & Vinogradov described a new species *Acanthocyclops mirnyi* (now known as *Diacyclops mirnyi*) from a number of freshwater lakes in the Bunger Hills. Borutzky (1962) subsequently recorded this species from the Vestfold Hills. When I came to study the freshwater invertebrates of the Vestfold Hills I had no reason to query this identification, indeed I extended its then known range to include the Larsemann Hills (Dartnall 1995b). Dartnall & Hollwedel (2007) recorded both *Diacyclops mirnyi* and *D. michaelseni* from the Falkland Islands while calling for a review of this genus. More recently Karanovic *et al.* (2013) described three new species – *D. kaupi* from Transkriptsii Gulf, an epishelf lake in the Bunger Hills close to where *D. mirnyi* was first recorded; *D. walkeri* from Pineapple Lake, an epishelf lake in the Vestfold Hills; and *D. joycei* from Lake Joyce, a permanently ice-covered lake in the McMurdo Sound region (table 1: Arthropoda: Crustacea: Cyclopoida). It is clear that a review of this genus is urgently needed.

The late David Frey considered all Antarctic identifications of *Macrothrix hirsuticornis* (Anomopoda: Arthropoda) as dubious as this is a northern hemisphere species (Frey 1987). Smirnov (1992) called for a review of this taxon, which had been reported from all sub-Antarctic islands, together with the South Orkney and South Shetland Islands and the northern Antarctic Peninsula (table 1: Arthropoda: Cladocera). Kotov's (2007) taxonomic review demonstrated that the southern hemisphere "*hirsuticornis*-like" complex actually equated to five related species – *M. flagellata* from Tasmania and Macquarie Island, *M. boergeni* from the Kerguelen Archipelago, *M. ruehei* from Îles Crozet, New Amsterdam and Prince Edward Islands, *M. sarsi* from the Cape region of South Africa and *M. oviformis* from southern South America, Falklands, South Georgia, South Orkney and South Shetland islands and the Antarctic Peninsula (table 1: Arthropoda: Cladocera) – leaving just the identity of the Heard Island *Macrothrix* to be determined. The inter-relationships of these five species is clearly a target for future study via molecular taxonomy. This technology should also be applied to *Boeckella poppei*, *Daphniopsis studeri*, *Branchinecta gaini*, *Ovalona weinecki*, *Acutuncus antarcticus*, *Adineta grandis*, *Philodina antarctica*, *P. gregaria*, *P. alata*, *Habrotrocha antarctica* and the *Notholca* cohort because of its "anomalous" distribution data.

Clearly modern developments in imaging, molecular taxonomy and computer analysis will reshape future re-appraisals of Antarctic limnology. Exciting as these new approaches will undoubtedly be, their very foundation lies in the work of the many scientists who have experienced and reported on all aspects of Antarctic limnology over the last 140 years.

ACKNOWLEDGEMENTS

A special thank-you to all those biologists who have cast a net into Antarctic and sub-Antarctic freshwaters on whose published work I have drawn in preparing this review: to the British Antarctic Survey, the Australian Antarctic Division and the South African National Antarctic Programme for logistic support during my five trips south: to the many expeditioners who so willingly helped me in the field: the taxonomic experts and colleagues I consulted over the years and the referees and editor of this Journal. Finally I thank my wife Dr Patricia Selkirk for her encouragement during this paper's long gestation and our daughters Dr Jennifer Selkirk-Bell who drew the map, and Ms Katherine Selkirk for her editing skills.

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(accepted 7 November 2017)

TABLE 1 — Distribution of the freshwater fauna of the south polar region. + the presence of a particular species at a given location; × an interloping terrestrial or brackish water species that has strayed into freshwater and continues alive in the "wrong" environment; ‡ a record that warrants verification, based on an unexpected observation and/or very few specimens; ? a questionable or dubious record; ( ) an anthropogenic/ introduced species; † a species that is no longer present or extinct at a location; numeral the number of recognised but not identified taxa, e.g., "the collector noted three unidentified species of nematode"; the total number of identified species found at each location is given for some groups in the table though this may not represent a true "total" if there are multiple entries of unidentified or partially identified records. A blank entry indicates an absence of data. A zero ('0') indicates definitive or suspected absence of that group.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
CNIDARIA	HYDRIDAE	*Hydra viridissima* Pallas, 1766						‡													
PLATYHELMINTHES	LECITHOEPITHELIATA	*Prorhynchus insularis* Beauchamp, 1940				+															
	NEORHABDOCOELA	*Neoophora* sp.										+									
	RHABDOCOELA	*Kalyptorhynchia* sp.										+									
	SERIATA	*Arthurdendyus vegrandis* Winsor & Stephens, 2005	x																		
		Curtisia seclusa (Beauchamp, 1940)				+															
		Duplominona amnica (Ball & Hay, 1977)	+																		
		Kontikia andersoni Jones, 1981	x																		
		unidentified species	1	1			5	4	2					1	1	1					1
		Number of species (Platyhelminthes)	4	1		2	5	4	2			2		1	1	1					1
ROTIFERA -	EPIPHANIDAE	*Epiphanes* cf. *daphnicola*	+																		
MONONOGONTA		*Epiphanes senta* (O F Müller, 1773)	+	+			+	+	+	+			+		+	+	+		+	+	+
		Rhinoglena frontalis Ehrenberg, 1853	+	+	+																
		Rhinoglena kutikovae de Smet & Gibson, 2008																	+		
	BRACHIONIDAE	*Brachionus angularis* Gosse, 1851																			+
		Brachionus bidentatus Anderson,1889								+											
		Brachionus bidentatus inermis Rousselet, 1906									+										
		Brachionus calyciflorus Pallas, 1766																		+	
		Brachionus havanaensis Rousselet, 1911								+											
		Brachionus quadridentatus Hermanns, 1783										+								+	
		Brachionus urceolaris O F Müller, 1773								+											+
		Kellicottia longispina (Kellicott, 1879)																			+
		Keratella americana Carlin, 1943								+											
		Keratella cochlearis (Gosse, 1851)								+			+			‡					+
		Keratella kostei de Paggi,1981						+													
		Keratella quadrata (O F Müller, 1786)											+								+

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	Mql	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
		Keratella sancta Russell, 1944	+		+																
ROTIFERA -	BRACHIONIDAE - cont	*Keratella* sp.								+											
MONONOGONTA		*Notholca foliacea* (Ehrenberg, 1838)																			+
		Notholca caudata Carlin, 1943						+													
		Notholca hollowdayi Dartnall, 1995		+	+																
		Notholca labis Gosse, 1887			+		+	+													
		Notholca salina Foche, 1961						+	+	+											
		Notholca squamula (O F Müller, 1786)	+		+								+								
		Notholca verae Kutikova, 1958														+			+		
		Notholca walterkostei de Paggi, 1982						+	+	+	+										
		N. walterkostei reducta Dartnall & Hollowday, 1985							+												
		Notholca sp.		+	+										+	+			+	+	
	EUCHLANIDAE	*Euchlanis dilatata* Ehrenberg, 1832					+														
		Euchlanis oropha Gosse, 1887						+	+			+									
		Euchlanis sp.		+																	
	MYTILINIDAE	*Lophocharis oxysternon* (Gosse, 1851)			+																
		Mytilina mucronata longicauda Dartnall & Hollowday, 1985						+													
	TRICHOTRIDAE	*Trichotria tetractis* (Ehrenberg, 1830)					+														
	COLURELLIDAE	*Colurella adriatica* Ehrenberg, 1831			+																
		Colurella colurus (Ehrenberg, 1830)			x	x				+											
		Colurella colurus compressa (Lucks, 1912)	+	+			+	+	+		+										
		Colurella geophyla Donner, 1951						+													
		Colurella obtusa (Gosse, 1886)						+													
		Colurella sp.						+													
		Lepadella acuminata (Ehrenberg, 1834)	+		+			+							+						
		Lepadella elliptica Wulfert, 1939																			+
		Lepadella intermedia Dartnall & Hollowday, 1985						+	+												
		Lepadella minuta Weber & Montet, 1918	+										+								
		Lepadella ovalis (O F Müller, 1786)						+													
		Lepadella patella (O F Müller, 1786)	+	+	+		+	+		+			+		+	+		+	+	+	

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
ROTIFERA -continued	BRACHIONIDAE - cont	*Lepadella patella oblonga* (Ehrenberg, 1834)			+			+	+												
		L. rhomboides signiensis Dartnall & Hollowday, 1985							+												
		Lepadella triptera (Ehrenberg, 1832)	+	+	+		+	+	+												+
		Lepadella sp.				+										+					+
	LECANIDAE	*Lecane closterocerca* (Schmarda, 1859)			+			+													x
		Lecane flexilis (Gosse, 1886)	+		+		+	+													
		Lecane hamata (Stokes, 1896)			+																
		Lecane latissima Yamamota, 1955						+													
		Lecane lunaris (Ehrenberg, 1832)						+	+	+											
		Lecane tenuiseta Harring, 1914			+																
		Lecane mawsoni Russell, 1959			+																
		Lecane sp.				+		+													
	PROALIDAE	*Bryceella stylata* (Milne,1886)						+													
		Proales fallaciosa Wulfert, 1937			+			+													
		Proales minima (Montet, 1915)			+																
		Proales reinhardti (Ehrenberg, 1834)			x											+			+		
		Proales sp.				+		+													
		Wulfertia sp.							‡												
	LINDIIDAE	*Lindia torulosa* Dujardin, 1841	+	+		x	+	+			+					+					
	NOTOMMATIDAE	*Cephalodella auriculata* (O F Müller, 1773)						+													
		Cephalodella catellina (O F Müller, 1786)	+		+			+	+	+											+
		Cephalodella delicata Wulfert, 1937	+		+			+	+												
		Cephalodella eva (Gosse, 1887)					+														
		Cephalodella evabroedae De Smet, 1988	+																		
		Cephalodella forficata (Ehrenberg, 1832)						+	+	+											
		Cephalodella forficula (Ehrenberg, 1830)	+		+							+									
		Cephalodella gibba (Ehrenberg, 1830)	+	+	+		+	+	+	+											
		Cephalodella megalocephala (Glasscott, 1893)	+					+	+												
		Cephalodella stenroosi Wulfert, 1937			+																
		Cephalodella sterae (Gosse, 1887)		+											+			+			

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
ROTIFERA - continued	NOTOMMATIDAE - cont.	*Cephalodella ventripes* (Dixon-Nuttall, 1901)		+											+						
		Cephalodella ventripes angustior Donner, 1950			+																
		Cephalodella sp.	+			+	+	2		+						2					+
		Eosphora najas Ehrenberg, 1830						+	+												
		Monommata sp,	+					+													
		Notommata cyrtopus Gosse, 1886			+																
		Notommata glyphura Wulfert, 1935	+	+	+			+													
		Pourriota carcharodonta De Smet, 2003			+																
		Resticula gelida (Harring & Myres, 1922)		+			+	+	+	+	+				+	+					
		Resticula nyssa Harring & Myres, 1924	+					+		+											
		Scaridium longicaudum (O F Müller, 1786)			+		+		+												
	TRICHOCERCIDAE	*Trichocerca bidens* (Lucks, 1912)	+		+																
		Trichocerca brachyura (Gosse, 1851)	+	+			+	+	+												
		Trichocerca obtusidens (Olofsson, 1918)			+																
		Trichocerca rattus (O F Müller, 1776)	+		+																
		Trichocerca rattus globosa Dartnall & Hollowday, 1985						+	+												
		Trichocerca tigris (O F Müller, 1786)	+					+													
	ASPLANCHNIDAE	*Polyarthra* sp.	+																		
	DICRANOPHORIDAE	*Dicranophorus forcipatus* (O F Müller, 1786)			+																
		Dicranophorus luetkeni (Bergendal, 1892)						+													
		Dicranophorus sp.		+			+														
		Encentrum forcipatum Dartnall, 1997														+					
		Encentrum gulo Wulfert, 1936					+														
		Encentrum heardensis Dartnall, 1995		+																	
		Encentrum limicola Otto, 1936			x																
		Encentrum lutra Wulfert, 1936					+						+								
		Encentrum martes Wulfert, 1939										+									
		Encentrum mustela (Milne, 1885)		+	+			+	+	+					+	+					
		Encentrum permolle (Gosse, 1886)			+																

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
ROTIFERA - continued	DICRANOPHORIDAE - cont.	*Encentrum permolle gigantheum* (Dartnall & Hollowday, 1985)	+						+												+
		Encentrum salinum Dartnall, 1997	+					+						+		+					
		Encentrum spatiatum Wulfert, 1936						+							+	+					
		Encentrum uncinatum (Milne, 1886)		+	+				+	+											
		Encentrum sp.								+	+					+					+
		Paradicranophorus sordidus Donner, 1968														+					
		Wierzejeskiella sp.	+																		
	TESTUDINELLIDAE	*Testudinella patina* (Hermann, 1783)			+																
		Testudinella sp.						+													
	FLOSCULARIIDAE	*Ptygura crystallina* (Ehrenberg, 1834)	+				+	+	+						+	+					
		Ptygura longicornis (Davis, 1867)					+														
		Ptygura melicerta Ehrenberg, 1832							+												
		Ptygura sp.		+	+											+					
	FILINIIDAE	*Filinia pejleri* Hutchinson, 1964			+																
		Filinia terminalis (Plate, 1886)	+																		
		Filinia sp.																			+
	COLLOTHECIDAE	*Collotheca companulata* Dobie, 1847							+												
		Collotheca ornata (Ehrenberg, 1832)					+														
		Collotheca ornata cornuta (Dobie, 1849)	+	+			+	+	+						+	+		+	+	+	+
		Collotheca sp.			+																+
		unidentified species							1							2					2
		Number of species (Rotifera: Monogononta)	33	21	43	4	22	48	30	21	6	4	7	1	11	21	1	3	7	6	19
ROTIFERA	ADINETIDAE	*Adineta barbata* Janson, 1893					x	x													
BDELLOIDEA		*Adineta gracilis* Janson, 1893						x													
		Adineta coatsae Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015							x	x						x					x
		Adineta editae Iakovenko, 2015							x	x											x

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
ROTIFERA - continued	ADINETIDAE - cont.	*Adineta emsliei* Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015		+						x							x				x
		Adineta grandis Murray, 1910							+					+	+	+	+		+	+	+
		Adineta vaga (Davis, 1873)	x	x																	x
		Adineta sp.	+		+		+	+						+	+	+			+		+
	HABROTROCHIDAE	*Habrotrocha angularis* (Murray, 1910)																			+
		Habtrotrocha antarctica Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015							+						+	+				+	+
		Habrotrocha constricta (Dujardin, 1841)		x				x													
		Habrotrocha elusa Milne, 1916															x				
		Habrotrocha sp.	+					2						+				+	+		+
	PHILODINIDAE	*Macrotrachela concinna* (Bryce, 1912)	x					x	x												
		Macrotrachela donneri Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015																			+
		Macrotrachela quadricornifera Milne, 1886														+					
		Macrotrachela sp.	2				+	2	+				+	+		+					+
		Mnobia russeola (Zelinka, 1891)														+					
		Mnobia sp.											+					+			
		Philodina alata Murray, 1910														+		+	+		+
		Philodina antarctica Murray, 1910									+										+
		Philodina dartnallis Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015							+	x											+
		Philodina gregaria Murray, 1910							+		+	+		+	+	+	+		+	+	+
		Philodina jeanneli Beauchamp, 1940			+																
		Philodina sp.	2		+		+	2	+		+		+	+	2	2		+	+		2
		Rotaria rotatoria (Pallas, 1766)	+	+			+	+													
	PHILODINAVIDAE	*Philodinavus* sp.																			+
		unidentified bdelloids			6		1			3									1		

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
		Number of species (Rotifera: Bdelloidea)	9	4	6		4	10	8	4	3	1	3	6	5	9	4	4	6	3	15
MICROGNATHOZOA		*Limnognathia maerski* Kristensen & Funch, 2000				+															
GASTROTRICHA	CHAETONOTIDAE	*Chaetonotus disjunctus* Greuter, 1917	+																		
		Chaetonotus sp.		+			+	>1	>2												+
		Lepidodermella squamata Dujardin, 1841	+																		
		Lepidodermella sp.						>1	>1	+											
		unidentified 'long spines' species							+												?
		Number of species (Gastrotricha)	2	1			1	2	3	1											1
NEMATODA	ARAEOLAIMIDA	*Plectus antarcticus* de Man, 1904									+					+			+		
		Plectus belgicae de Man, 1904									+										
		Plectus frigophilus Kiryanova, 1958														+			+		+
		Plectus globilabiatus Kiryanova, 1958																	+		
		Plectus parientinus Bastain, 1865								+	+										
		Plectus parvus Bastain, 1865								+											
		Plectus sp.	+	+				+	+	2						+		+	+		2
	CHROMADORIDA	*Teratocephalus* cf. *lirellus*								+											
		Teratocephalus tilbrooki Maslen, 1979										x									
		Teratocephalus sp.								2											
	DORYLAIMIDA	*Dorylaimus* sp.	+								2										
		Enchodelus sp.		+																	
		Eudorylaimus antarcticus (Steiner, 1916)									+										
		Eudorylaimus frigidus (Steiner, 1916)				+															
		Eudorylaimus gaussi (Steiner, 1916)				+															
		Eudorylaimus spaulli Loof, 1975								+											
		Eudorylaimus sp.	+					+	+	+											
		Mesodorylaimus sp.	+	+				+			3										
		Mononchus gerlachei de Man, 1904				+					+										
		Mononchus sp.	+							+		+									
	ENOPLIDA	*Enoplodes stewarti* Nicholas, 1993	+																		
		Prismatolaimus sp.	x																		

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
NEMATODA - cont.	MONHYSTERIDA	*Geomonhystera antarcticola* Andrássy, 1998																	+		
		Halomonhystera continenalis Andrássy, 2006														x					
		Monhystera sp.		+				+	+	2											
	MONONCHIDA	*Coomansus gerlachei* (de Man, 1904)							+	+											
		Coomansus sp.						+													
		Paramylonchulus sp.										x									
	RHABDITIDA	*Cervidellus* sp.	+																		
	TYLENCHIDA	*Antarctenchus motililus* Ghosh, Chatterjee, Mitra & De, 2005										x									
		Aphelenchoides sp.								2		x									
		Ditylenchus sp.								+											
		Rotylenchus sp.										x									
		Tylenchorhynchus sp.										x									
		Tylenchus sp.						+													
		unidentified species		1		3	6			1				1	2	2				2	1
		Number of species (Nematoda)	8	5		6	6	6	4	15	7	7		1	2	5		1	5	2	4
ANNELIDA -	ACANTHRODRILIDAE	*Microscolex kerguelarum* (Grube, 1877)			x		x														
DIPLOTESTICULATA		*Microscolex macquariensis* (Beddard, 1896)	x																		
	LUMBRICIDAE	*Dendrodrilus rubidus* (Savigny, 1826)		(x)																	
		Eiseniella tetraedra (Savigny, 1826)	(†)		(x)																
TUBIFICATA	NAIDIDAE	*Nais elinguis* Müller, 1774	+		+																
		Vejdovskyella sp.					+														
	PHREODRILIDAE	*Astacopsidrilus campbellianus* (Benham, 1909)	+																		
		Nesodrilus crozetensis (Michaelsen, 1905)				+		+													
		Nesodrilus kerguelenensis (Michaelsen, 1903)			+		+														
	TUBIFICIDAE	*Ainudrilus dartnalli* Erséus & Grimm, 2002						+													
		Aulodrilus pigueti Kowalewski, 1914								+											
		Macquaridrilus bennettae Jamieson, 1968	+																		
		Rhyacodrilus coccineus Vejdovský, 1875				+		+													
	ENCHYTRAEIDAE	*Cernosvitoviella* sp.	+																		

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
ANNELIDA - cont.	ENCHYTRAIDAE - cont.	*Cognettia antipodum* (Benham, 1905)	+																		
		Enchytraeus albidus Henle, 1837						x													
		Lumbricillus antarcticus Stephenson, 1932						+													
		Lumbricillus healyae Rodrigues & Rico, 2008								+											
		Lumbricillus incisus Liang & Wang, 1997								+											
		Lumbricillus lineatus (Müller, 1774)	(x)																		
		Lumbricillus macquariensis Benham, 1915	x																		
		Lumbricillus sp. 1					+														
		Lumbricillus sp. 2								+											
		Mesenchytraeus sp.	(+)																		
		unknown enchytraeid								2		‡									
		Number of species (Annelida)	9		3	2	4	5		4	0	0	0	0	0	0	0	0	0	0	0
TARDIGRADA -	ECHINISCIDAE	*Echiniscus jenningsi* Dastych, 1984						x	x												
HETEROTARDIGRADA		*Echiniscus macronyx* Richters, 1907						x													
		Echiniscus spp.					x			x	x	x									
		Echinoscoides sp.										x									
		Mopsechiniscus imberis (Richters, 1908)						x													
TARDIGRADA -	HYPSIBIIDAE	*Acutuncus antarcticus* (Richters, 1904)		+					+	+					+	+					+
EUTARDIGRADA		*Adropion greveni* Dastych, 1984								+	+										
		Adropion cf. *greveni*							+												
		Diphascon langhovdense (Sudzuki, 1964)										x									
		Diphascon pengue (Marcus, 1936)							+		+			+							+
		Diphascon sp.							+		+					+					+
		Hypsibius dujardin (Doyère, 1840)	x				x				x										
		Hypsibius sp.										x			x	x					
		Isohypsibius asper (Murray, 1906)							+	+	+										
		Isohypsibius laevis McInnes, 1995							+												
		Isohypsibius papillifer (Murray, 1905)							+												
		Isohypsibius sp.					+			+						+					
		Mesobiotus furciger Murray, 1907							x		x										
		Ramajendas frigidus Pillato & Bind, 1991									x										

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
TARGIGRADA - cont.	MACROBIOTIDAE	*Ramazzottius oberhaeuseri* (Doyère, 1840)									x										+
		Ramazzottius sp.									x										
		Dactylobiotus cf. *ambiguus*							+	+	+										
		Dactylobiotus sp.	+	+			+	+													
		Macrobiotus cf. *liviae*							x												
		Macrobiotus polaris Murray, 1907										x									x
		Macrobiotus sp.						2	x			x		x		x				+	+
		Murrayon hastatus/pullari	x																		
	MILNESIIDAE	*Milnesium antarcticum* Tumanov, 2006								x	x	x									
		Milnesium cf. *tardigradum*					x		x						x						
		unidentified species											x								
		Number of species (Tardigrada)	3	2			5	6	13	7	11	7	1	2	3	5				1	6
ARTHROPODA -	COLEOPTERA	*Lancetes angusticollis* (Curtis, 1839)						+													
INSECTA	DIPTERA	*Ephydrella macquariensis* Wormersley, 1937	+																		
		Limnophyes pusillus Eaton, 1875			(+)	(+)	(+)														
		Limnophyes sp.						+													
		Parochlus crozetensis Serra-Tosio, 1986				+															
		Parochlus steinenii (Gercke, 1889)						(+)		(+)											
		Schoenophilus pedestris Lamb, 1909	+																		
		Trimicra pilipes Fabricius, 1787	+																		
		Number of species (Insecta)	3		1	2	1	3		1		0	0	0	0	0	0	0	0	0	0
ARTHROPODA -	ANOSTRACA	*Branchinecta gaini* Daday de Dées, 1901						+	+	+	+										
CRUSTACEA	CLADOCERA	*Alona quadrangularis* (O F Müller, 1785)	+																		
		Camptocercus aloniceps Ekman, 1901						+													
		Chydorus patagonicus Ekman, 1900	+					+													
		Chydorus sphaericus (O F Müller, 1785)			+	+		+	+												
		Daphnia gelida (Brady, 1918)	+																		
		Daphniopsis studeri Rühe, 1914		+	+	+	+						+	+	+	+					
		Ilyocryptus brevidentatus Ekman, 1905						+	+												
		Macrothrix boergeni Studer, 1878			+																

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
ARTHROPODA - cont.	CLADOCERA - cont.	*Macrothrix flagellata* (Smirnov & Timms, 1983)	+																		
		Macrothrix oviformis Ekman, 1900						+	+	+	+										
		Macrothrix ruehei Kotov, 2007				+	+														
		Macrothrix sp.		+																	
		Ovalona weinecki (Studer, 1878)	+	+	+		+	+	+	+											
		Pleuroxus macquariensis Frey, 1993	+																		
		Pleuroxus truncatus Müller, 1785						(?)													
		Pleuroxus wittsteini Studer, 1878		+	+		+														
	OSTRACODA	*Candona* sp.						+													
		Chlamydotheca pestai (Graf, 1931)						+													
		Cypretta cf. *seurati*	+																		
		Eucypris corpulenta (Sars, 1895)			+																
		Eucypris fontana (Graf, 1931)						+	+												
		Eucypris virens Jurine, 1820	+		+																
		Ilyodromus kerguelensis Müller, 1906			+	+	+														
		Notiocypridopsis frigogena (Graf, 1931)						+	+												
		Tanycypris sp.						+													
ARTHROPODA -	CALANOIDA	*Boeckella poppei* (Mrázek, 1901)						+	+	+	+			+							
CRUSTACEA		*Boeckella michaelseni* (Mrázek, 1901)						+													
		Boeckella brevicaudata (Brady, 1875)	+	+	+																
		Boeckella vallentini (Scott, 1914)			+	+	+														
		Boeckella sp.																			+
		Gladioferens antarcticus Bayly, 1994																	+		
		Parabroteas sarsi (Daday de Dées, 1901)						+	+												
		unidentified Calanoid																			+
	CYCLOPOIDA	*Acanthocyclops michaelseni* (Mrázek, 1901)			+																
		Acanthocyclops robustus (Sars, 1863)			+																
		Acanthocyclops vernalis Fischer, 1853			+																
		Diacyclops joycei Karanovic, Gibson, Hawes, Andersen & Stevens, 2013																			+

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
ARTHROPODA - cont.	CYCLOPOIDA - cont.	*Diacyclops kaupi* Karanovic, Gibson, Hawes, Andersen & Stevens, 2013																	+		
		Diacyclops michaelseni (Mrázek, 1901)			+																
		Diacyclops mirnyi (Borutsky & Vinogradov, 1957)													+	+			+		
		Diacyclops walkeri Karanovic, Gibson, Hawes, Andersen & Stevens, 2013														+					
		Mixocyclops crozensis Kiefer, 1944				+															
		Paracyclops chiltoni (Thompson, 1882)			+	+															
	HARPACTICOIDA	*Antarctobiotus koenigi* (Pesta, 1928)						+													
		Antarctobiotus robustus Richters, 1907			+	+															
		Bryocamptus zschokkei Schmeil, 1893			+																
		Canthocamptidae spp.						2													1
		Epactophanes richardi Mrázek, 1893		+	+	+	+														
		Marionobiotus jeanneli Chappuis, 1940	+		+		+														
		Marionobiotus sp.	+																		
		Tigriopus angulatus Lang, 1933	x		x	x	x														
		Zaus contractus Thompson, 1883	?																		
		unidentified harpacticoid								+											
	AMPHIPODA	*Kergueleniola macra* Ruffo, 1970			‡																
		Pseudingolfiella possessionis de Smet, 2015				+															
		unidentified species						‡													
	ISOPODA	*Iais* sp.	+																		
		Number of species (Arthropoda: Crustacea)	13	6	20	12	9	16	9	5	3		1	2	2	3			3		5
ARTHROPODA -	ACARIDIDA	*Acarus siro* Linnaeus, 1758										(x)									
ARACHNIDA		*Algophagus antarcticus* Hughes, 1955		+																	
		Algophagus brachytarus Marshall, O'Connor & Pugh 2003					x														
		Algophagus laticollaris Fain, 1975					x														
		Algophagus macrolithus Marshall, O'Connor & Pugh, 2003					x														
		Suidasia nesbitti Hughes, 1948										x									

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	MeM
ARTHROPODA - cont.		*Tyrophagus longior* (Grevais, 1844)										x									
		unknown larvae	2	1				1	1												
	ORIBATIDA	*Alaskozetes antarcticus* (Michael, 1903)		x			x		x	x	x										
		Alaskozetes antarcticus grandjeani (Dalenius, 1958)	x																		
		Austroppia crozetensis (Richters, 1908)					x														
		Dometorina marionensis Van Pletzen & Kok, 1971					x														
		Edwardzetes elongatus Wallwork, 1966						x													
		Galumna alata (Hermann, 1804)						x													
		Globoppia intermedia longiseta Wallwork, 1970						x													
		Halozetes belgicae (Michael, 1903)	x	x				x	x												
		Halozetes sp.										x									
		Haplochthonius antarcticus Sanyal, Basak & Barman, 2002										x									
		Haplochthonius longisetosus Sanyal, Basak & Barman, 2002										x									
		Haplochthonius maitri Sanyal, Basak & Barman, 2002										x									
		Macquarioppia striata (Wallwork, 1963)		x			x														
		Magellozetes antarcticus (Michael, 1895)						x													
		Maudheimia petronia Wallwork, 1962										x									
		Oppia crozetensis (Richters, 1908)					x														
		Platynothrus skottsbergii Tragårdh, 1931						x													
		Podacarus auberti occidentalis Wallwork,1966		x																	
		Trimalaconothrus flagelliformis Wallwork, 1970						x													
	GAMASIDA	*Gamasellus racovitzai* (Trouessart, 1903)							x	x											
ARTHROPODA -		*Hypoaspis oblonga* Halbert, 1915										x									
ARACHNIDA		*Proctolaelaps antarcticus* Sanyal & Gupta, 2005										x									
		unknown larvae	x																		
	PROSTIGMATA	*Bryobia praetiosa* CL Koch, 1836						(x)													
		Chelacaropsis moorei Baker, 1949										x									
		Nanorchestes antarcticus Strandtmann, 1963										x									

Table 1 — cont.

Phylum - (sub-Phylum)	Order or Family	Species	MqI	HI	K	C	PE	SG	SO	SS	AP	Sch	TH	PCM	LH	VH	Has	OH	BH	WL	McM
ARTHROPODA - cont.	PROSTIGMATA - cont.	*Paratydeus* sp.										x									
		Peregrinacarus reticulatus Bartsch, 1999					+														
		Pronematus sp.										x									
		Raphignathus sp.										x									
		Stereotydeus villosus (Trouessart, 1903)								x											
		Tetranynchus sp.						x													
		Number of species (Arthropoda: Arachnida)	5	6			9	10	4	3	1	14	0	0	0	0	0	0	0	0	0
CHORDATA -	SALMONIDAE	*Oncorhynchus kisutch* (Walbaum, 1792)			(+)																
OSTEICHTHYES		*Oncorhynchus mykiss* (Walbaum, 1792)			(†)			(†)													
		Oncorhynchus tshawytscha (Walbaum, 1792)			(†)																
		Salmo salar Linnaeus, 1758			(+)																
		Salmo trutta Linnaeus, 1758			(+)	(+)	(†)														
		Salvelinus alpinus (Linnaeus, 1758)			(+)																
		Salvelinus fontinalis (Mitchill, 1814)			(+)	(+)	(†)														
		Salvelinus namaycush (Walbaum, 1792)			(†)																
		Number of species (Chordata: Osteichthes)	0	0	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CHORDATA -		*Anas eatoni* (Sharpe, 1875)			+	+															
AVES		*Anas flavirostris* Vieillot, 1816						+													
		Anas georgica Gmelin, 1789						+													
		Anas gibberifrons Müller 1842	+																		
		Anas platyrhynchos Linnaeus, 1758	(+)		(+)																
		Anas superciliosa Gmelin, 1789	+																		
		Number of species (Chordata: Aves)	3	0	2	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 1 — Synonyms and mistaken identities. Care should be exercised in using this list of synonyms and mistaken identities away from this study. Some of the mistaken identities remain legitimate species both elsewhere and in the Antarctic while other records are only correct at specifc locations. For example the anomopodan previously identified as *Macrothrix hirsuiticornis* is now *M. flagellata* at Macquarie Island, *M. boergeni* at Kerguelen, *M. ruehei* at Crozet and the Prince Edward Islands and *M. oviformis* at South Georgia, the South Orkney islands, South Shetland Islands and down the Antarctic Peninsula. *Macrothrix hirsuiticornis*, a valid species in the northern hemisphere, is entered five times in the Synonyms and mistaken identity column. *Daphniopsis studeri* is a valid identification of the cladoceran present on Heard Island, Kerguelen, Crozet, the Prince Edward Islands, the Prince Charles Mountains, and the Larsemann and Vestfold Hills. Several authors have implied that this is the cladoceran present on Macquarie Island when the cladoceran there is *Daphnia gelida*. *Daphniopsis studeri* is consequently listed as a mistaken identity for *Daphnia gelida* but only for Macquarie island. This list also contains synonyms and mistaken identities for a number of brackish and terrestrial species that were considered as possible freshwater inhabitant but proved not to be.

Synonyms and mistaken identities	**Current identifications**
Acanthocyclops mirnyi Borutsky & Vinogradov, 1957	*Diacyclops mirnyi* (Borutsky & Vinogradov, 1957)
Acanthodrilus georgianus Michaelsen, 1888	*Microscolex georgianus* (Michaelsen, 1888)
Acanthodrilus kerguelarum Grube, 1877	*Microscolex kerguelarum* (Grube, 1877)
Acanthodrilus kerguelenensis Lankester, 1879	*Microscolex kerguelarum* (Grube, 1877)
Acanthodrilus macquariensis Beddard, 1896	*Microscolex macquariensis* (Beddard, 1896)
Adineta barbata Janson, 1893	*Adineta coatsea* Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015
Adineta gracilis Janson, 1893	*Adineta editae* Iakovenko, 2015
Adineta sp. A from Heard Island	*Adineta emslie* Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015
Allolobophora tenuis Eisen, 1874	*Dendrodrilus rubidus* (Savigny, 1824)
Alona bukobensis subantarctica Ekman, 1905	*Ovalona weinecki* (Studer, 1878)
Alona diaphana King, 1853	*Ovalona weinecki* (Studer, 1878)
Alona rectangula Sars, 1862	*Ovalona weinecki* (Studer, 1878)
Alona subantarctica Sars, 1909	*Ovalona weinecki* (Studer, 1878)
Alona weinecki Studer, 1878	*Ovalona weinecki* (Studer, 1878)
Alona spp.	*Ovalona weinecki* (Studer, 1878)
Anisomera claussi Müller, 1884	*Lancetes angusticollis* (Curtis, 1839)
Antholaimus antarcticus (Steiner, 1916)	*Eudorylaimus antarcticus* (Steiner, 1916)
Atthyella koenigi Pesta, 1928	*Antarctobiotus koenigi* (Pesta, 1928)
Bimastos tenuis (Eisen, 1874)	*Dendrodrilus rubidus* (Savigny, 1826)
Boeckella brasiliensis Poppe & Mrázek, 1895	*Boeckella poppei* (Mrázek, 1901)
Boeckella dubia Daday de Dées, 1901	*Boeckella poppei* (Mrázek, 1901)
Boeckella entzii Daday de Dées, 1901	*Boeckella poppei* (Mrázek, 1901)
Boeckella pygmaea Daday de Dées, 1901	*Boeckella michaelsini* (Mrázek, 1901)
Boeckella silvestri Daday de Dées, 1901	*Boeckella poppei* (Mrázek, 1901)
Boeckellina michaelsini Mrázek, 1901	*Boeckella michaelsini* (Mrázek, 1901)
Branchinecta granulosa Pesta, 1933	*Branchinecta gaini* Daday de Dées, 1901
Branchinecta sp.	*Branchinecta gaini* Daday de Dées, 1901
Branchiura pleurotheca Benham, 1907	*Rhyacodrilus coccineus* (Vejdovsky, 1875)
Callidina angularis Murray, 1910	*Habrotrocha angularis* (Murray, 1910)
Callidina constricta Dujardin, 1841	*Habrotrocha constricta* (Dujardin, 1841)
Callidina habita Bryce, 1894	*Macrotrachela donneri* Iakovenko *et al.*, 2015
Callidina papillosa Thompson, 1892	*Macrotrachela papillosa* Thompson, 1892
Callidina tridens Milne, 1886	*Habrotrocha tridens* (Milne, 1886)
Callidina spp.	various genera
Camptocercus spp.	*Camptocercus aloniceps* Ekman, 1901
Canadona ahlefeldi Studer, 1879	*Ilyodromus kerguelensis* G W Müller, 1906
Canthocamptus antarcticus Richters, 1907	*Epactophanes richardi antarcticus* Mrázek, 1893
Canthocamptus antarcticus Richters, 1907	*Epactophanes richardi* Mrázek, 1893
Canthocamptus robustus Richters, 1907	*Antarctobiotus robustus* (Sars, 1863)
Centropagus brevicaudatus Brady, 1875	*Boeckella brevicaudata* (Brady, 1875)
Chaetonotus squamatus Dujardin 1841	*Lepidodermella squamata* (Dujardin, 1841)
'Chydorid' spp.	*Ovalona weinecki* (Studer, 1878)
Chydorus maquariensis Brady, 1918	*Chydorus patagonicus* Ekman, 1900
Chydorus minutus Thomson, 1878	*Chydorus patagonicus* Ekman, 1900
Chydorus sphaericoides Sars, 1909	*Chydorus sphaericus* Ekman, 1900
Collotheca gracilipes Edmondson, 1939	*Collotheca companulata* (Dobie, 1849)

Appendix 1 — cont.

Synonyms and mistaken identities	Current identifications
Colurus amblytelus Gosse, 1886	*Colurella colurus* (Ehrenberg, 1830)
Cyclops bospini Studer, 1878	*Acanthocyclops robustus* (Sars, 1863)
Cyclops krillei Studer, 1878	*Acanthocyclops robustus* (Sars, 1863)
Cyclops michaelseni Mrázek, 1901	*Acanthocyclops michaelseni* (Mrázek, 1901)
Cyclops robustus vernalis Fischer, 1853 after Smith & Sayers, 1971	*Acanthocyclops vernalis* (Fischer, 1853)
Cypretta sp.	*Cypretta cf seurati*
Cypridopsis frigogena Graf, 1931	*Notiocypridopsis frigogena* (Graf, 1931)
Cypris fontana Graf, 1931	*Eucypris fontana* (Graf, 1931)
Daphnia carinata King, 1852	*Daphnia gelida* (Brady, 1918)
Daphnia sarsi Daday de Dées, 1902	*Daphnia gelida* (Brady, 1918)
Daphnia studeri Brehm, 1940	*Daphniopsis studeri* Rühe, 1914
Daphniopsis spp.	*Daphniopsis studeri* Rühe, 1914
Daphniopsis studeri Rühe, 1914	*Daphnia gelida* (Brady, 1918)
Deguernea antarctica Thomson, 1895	*Boeckella brevicaudata* (Brady, 1875)
Dendrobaena rubida Savigny, 1826	*Dendrodrilus rubidus* (Savigny, 1826)
Diacyclops michaelseni (Mrázek, 1901) after (Morton, 1985)	*Acanthocyclops michaelseni* (Mrázek, 1901)
Diaschiza sp.	*Cephalodella catellina* (O.F. Müller, 1786)
Diaschiza tenuior Gosse, 1886	*Cephalodella catellina* (O.F. Müller, 1786)
Dicranophorus permollis giganthea Dartnall & Hollowday, 1985	*Encentrum permolle gigantheum*(Dartnall & Hollowday, 1985)
Diglena uncinata Milne, 1886	*Encentrum uncinatum* (Milne, 1886)
Diphascon alpinus/pinguis	*Diphascon pingue* (Marcus, 1936)
Diphascon cf. *greveni*	*Adropion cf greveni*
Diphascon scoticus Murray 1905	*Adropion greveni* Dastych, 1984
Dorylaimus frigidus Steiner, 1916	*Eudorylaimus frigidus* (Steiner, 1916)
Dorylaimus gaussi Steiner, 1916	*Eudorylaimus gaussi* (Steiner, 1916)
Encentrum brevifulcrum Dartnall, 1997	*Paradicranophorus sordidus* Donner, 1968
Enchytraeus antipodum Benham, 1905	*Cognettia antipodum* (Benham, 1905)
Enchytraeus colpites Stephenson, 1932	*Lumbricillus colpites* (Stephenson, 1932)
Enchytraeus monochaetus Michaelsen, 1888	*Grania monochaeta* (Michaelsen, 1888)
Epiphanes sp. (Macquarie Island)	*Epiphanes daphnicola* Thompson, 1892
Erioptera pilipes Fabricius, 1787	*Trimicra pilipes* (Fabricius, 1787)
Erioptera pilipes macquariensis Alexander, 1962	*Trimicra pilipes* (Fabricius, 1787)
Euchlanis dilatata parva Rousselet, 1892	*Euchlanis oropha* Gosse 1887
Eucypris sp.	*Eucypris fontana* (Graf, 1931)
Euplanaria seclusa de Beauchamp, 1940	*Curtisia seclusa* (de Beauchamp, 1940)
Filinia maior (Colditz, 1924)	*Filinia terminalis* (Plate, 1886)
Filinia terminalis kergueleniensis Lair & Koste, 1984	*Filinia pejleri* Hutchinson, 1964
Floscularia cornuta Ehrenberg, 1832	*Collotheca ornata cornuta* (Ehrenberg, 1832)
Gigantella sarsi (Ekman, 1905)	*Parabroteas sarsi (*Daday de Dées, 1901)
Guernea antarctica Thomson, 1895	*Boeckella brevicaudata* (Brady, 1875)
Guernella antarctica Mrázek, 1904	*Boeckella brevicaudata* (Brady, 1875)
Habrotrocha constricta (Murray, 1910)	*Habrotrocha antarctica* Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015
Halirytus amphibius Eaton, 1875	*Telmatogeton amphibius* (Eaton, 1875)
Halirytus macquariensis Brundin, 1962	*Telmatogeton macquariensis* (Brundin, 1962)
Harpacticus brevicornis Giesbrecht, 1902	*Tigriopus angulatus* Lang, 1933
Harpacticus fulvus Brady, 1875	*Tigriopus angulatus* Lang, 1933
Hesperodrilus campbellianus Michaelsen, !924	*Astacopsidrilus campbellianus* (Benham, 1909)
Hesperodrilus crozetensis Michaelsen, 1905	*Nesodrilus crozetensis* (Michaelsen, 1905)
Hesperodrilus kerguelensis Michaelsen, 1903	*Nesodrilus kerguelensis* (Michaelsen, 1903)
Hydatina senta Ehrenberg, 1830	*Epiphanes senta* (O.F. Müller, 1773)
Hydra viridis Linnaeus, 1767	*Hydra viridissima* Pallas, 1766
Hypsibius arcticus Murray, 1907	*Acutuncus antarcticus* (Richters, 1904)
Hypsibius chilensis (Plate, 1889)	*Diphascon langhovdense* (Sudzuki, 1964)
Hypsibius oberhaeuseri (Doyére, 1840)	*Ramazzottius oberhaeuseri* (Doyére, 1840)
Hypsibius papillifer (Murray, 1905)	*Isohypsibius papillifer* (Murray, 1905)
Hypsibius (Isohypsibius) renaudi Ramazzotti, 1972	*Ramajendas frigidus* Pillato & Binda, 1991

Appendix 1 — cont.

Synonyms and mistaken identities	Current identifications
Ilyocryptus spp.	*Ilyocryptus brevidentatus* Ekman, 1905
Isohypsibius granulifer Thulin, 1928	*Isohypsibius asper* (Murray, 1906)
Isohypsibius renaudi Ramazzotti,1972	*Ramajendas frigidus* Pillato & Binda, 1991
Keratella heywoodi Dartnall, 2005	*Keratella kostei* Paggi, 1981
Kerguelenella macra Ruffo, 1970	*Kergueleniola macra* Ruffo, 1970
Lancetes claussi (Müller, 1884)	*Lancetes angusticollis* (Curtis, 1839)
Lecane glypta Harring & Myres, 1926	*Lecane flexilis* (Gosse, 1889)
Lecane mawsoni Russell, 1959	*Lecane* cf. *closterocerca*
Lepadella oblonga (Ehrenberg, 1834)	*Lepadella patella oblonga* (Ehrenberg, 1834)
Limnocalanus sarsi Daday de Dées, 1901	*Parabroteus sarsi* (Daday de Dées, 1901)
Lumbricillus intermedius (Benham, 1909)	*Lumbricillus macquariensis* Benham, 1905
Lumbricillus kerguelarum Grube, 1877	*Microscolex kerguelarum* (Grube, 1877)
Macrobiotus ambiguus Murray, 1907	*Dactylobiotus ambiguus* (Murray, 1907)
Macrobiotius arcticus Murray, 1907	*Acutuncus antarcticus* (Richters, 1904)
Macrobiotus furciger Murray, 1907	*Mesobiotus furciger* (Murray, 1907)
Macrobiotus hastatus/pullari	*Murrayon hastatus/pullari*
Macrothrix ciliata Vávra, 1900	*Macrothrix oviformis* Ekman, 1900
Macrothrix hirsuticornis Norman & Brady, 1861 at K	*Macrothrix boergeni* Studer,1878
Macrothrix hirsuticornis Norman & Brady, 1861 at MqI	*Macrothrix flagellata* (Smirnov & Timms, 1983)
Macrothrix hirsuticornis Norman & Brady, 1861 at SG, SO, SS & AP	*Macrothrix oviformis* Ekman, 1900
Macrothrix hirsuticornis Norman & Brady, 1861 at C & PE	*Macrothrix ruehei* Kotov, 2007
Macrothrix hirsuticornis Norman & Brady, 1861 at South Africa	*Macrothrix sarsi* Kotov, 2007
Macrothrix inflata Daday de Dées, 1902	*Macrothrix oviformis* Ekman, 1900
Macrothrix odontocephala Dadayde Dées, 1902	*Macrothrix oviformis* Ekman, 1900
Macrothrix propinqua Sars, 1909	*Macrothrix oviformis* Ekman, 1900
Macrotrachela habita (Bryce, 1894)	*Macrotrachela donneri* Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015
Macrotrachela insolita De Koning, 1947	*Macrotrachela donneri* Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015
Marionina aestuum Stephenson, 1932	*Lumbricillus aestuum* (Stephenson, 1932)
Marionina antipodum (Benham, 1905)	*Cognettia antipodum* (Benham, 1905)
Marionina grisea Stephenson, 1932	*Lumbricillus griseus* (Stephenson, 1932)
Marionina werthi Michaelsen, 1905	*Lumbricillus werthi* (Michaelsen, 1905)
Michaelsena monochaetus (Michaelsen, 1888)	*Grantia monochaeta* (Michaelsen, 1888)
Microscolex luykeni Michaelsen, 1905	*Microscolex crozetensis* (Michaelsen, 1905)
Milnesium tardigradum Doyére, 1840	*Milnesiun* cf. *tardigradum*
Minona amnica Ball & Hay, 1977	*Duplominona amnica* (Ball & Hay, 1977)
Moraria spp.	*Epactophanes richardi* Mrázek, 1893
Neorhabdocoela sp.	*Neoophora* sp.
Notholca jugosa (Gosse, 1889)	*Notholca squamula* (O F Müller, 1786)
Notholca verae Kutikova, 1958	*Notholca walterkostei* de Paggi, 1982
Notiodrilus crozetensis Michaelsen, 1905	*Microscolex crozetensis* (Michaelsen, 1905)
Notiodrilus kerguelarum Michaelsen, 1900	*Microscolex kerguelarum* (Grube, 1877)
Notiodrilus kerguelenensis Michaelsen, 1910	*Microscolex kerguelarum* (Grube, 1877)
Notiodrilus luykeni Michaelsen, 1905	*Microscolex crozetensis* (Michaelsen, 1905)
Notiodrilus macquariensis Michaelsen, 1900	*Microscolex macquariensis* (Beddard, 1896)
Pachydrilus maximus Michaelsen, 1888	*Lumbricillus maximus* (Michaelsen, 1888)
Pachydrilus georgianus Michaelsen, 1888	*Marionina georgiana* (Michaelsen, 1888)
Pachydrilus intermedius Michaelsen, 1923	*Lumbricillus macquariensis* (Benham,1905)
Pachydrilus macquariensis Benham, 1915	*Lumbricillus macquariensis* (Benham,1905)
Pachydrilus maritimus Ude, 1896	*Lumbricillus maritimus* (Ude, 1896)
Pachydrilus maximus Michaelsen, 1888	*Lumbricillus maximus* (Michaelsen, 1888)
Pachydrilus werthi Michaelsen, 1905	*Lumbricillus werthi* (Michaelsen, 1905)
Paraboeckella brevicaudata (Brady, 1875) in Mrásek, 1901	*Boeckella brevicaudata* (Brady, 1875)
Parabroteus michaelseni Mrázek, 1901	*Parabroteus sarsi* (Daday de Dées, 1901)
Paracyclops fimbriatus (Fischer, 1853)	*Paracyclops chiltoni* (Thompson, 1882)

Appendix 1 — cont.

Synonyms and mistaken identities	Current identifications
Peracantha truncata (Müller, 1785) in Smith & Sayers, 1971	*Pleuroxus truncatus* (Müller, 1785)
Philodina roseola Ehrenberg, 1832	*Philodina gregaria* Murray, 1910
Philodina sp. A from Signy Island	*Philodina dartnallis* Iakovenko, Smykla, Convey, Kašparová, Kozeretska, Trokhymets, Dykyy, Plewka, Devetter, Duriš & Janko, 2015
Phreodrilus campbellianus Benham, 1909	*Astacopsidrilus campbellianus* (Benham, 1909)
Phreodrilus crozetensis Michaelsen, 1905	*Nesodrilus crozetensis* (Michaelsen, 1905)
Phreodrilus kerguelensis Michaelsen, 1923	*Nesodrilus kerguelensis* (Michaelsen, 1903)
Pleurotrocha sp.	*Encentrum permolle gigantheum* Dartnall & Hollowday, 1985
Pleuroxus aduncus Jurine, 1820	*Pleuroxus wittsteini* Studer, 1878
Pleuroxus scopulifer Daday De Dées, 1903	*Pleuroxus wittsteini* Studer, 1878
Pleuroxus scopuliferus Ekman, 1900	*Pleuroxus wittsteini* Studer, 1878
Proales daphnicola Thompson, 1892	*Epiphanes daphnicola* (Thompson, 1892)
Pseudobiotus cf. *augusti*	*Isohypsibius laevis* McInnes, 1995
Pseudoboeckella anderssonorum Ekman, 1905	*Boeckella michaelseni* (Mrázek, 1901)
Pseudoboeckella brevicaudata (Mrázek, 1905)	*Boeckella brevicaudata* (Brady, 1875)
Pseudoboeckella entzii Daday De Dées, 1901	*Boeckella poppei* (Mrázek, 1901)
Pseudoboeckella klutei Brehm, 1926	*Boeckella poppei* (Mrázek, 1901)
Pseudoboeckella poppei Mrázek, 1901	*Boeckella poppei* (Mrázek, 1901)
Pseudoboeckella pygmaea Daday De Dées, 1902	*Boeckella michaelseni* (Mrázek, 1901)
Pseudoboeckella remotissima Brehm, 1953	*Boeckella brevicaudata* (Brady, 1875)
Pseudoboeckella silvestrii Daday De Dées, 1901	*Boeckella poppei* (Mrázek, 1901)
Pseudoboeckella vallentini Scott, 1914	*Boeckella vallentini* (Scott, 1914)
Pseudoboeckella volucris Kiefer, 1944	*Boeckella vallentini* (Scott, 1914)
Psychoda severini parthenogenetica Tonnoir, 1940	*Psychoda parthenogenetica* Tonnoir, 1940
Ramajendas renaudi (Ramazzotti,1972)	*Ramajendas frigidus* Pillato & Binda, 1991
Rhinoglena fertoeensis Varga, 1928	*Rhinoglena kutikovae* De Smet & Gibson, 2008
Salmo gairdneri (Richardson, 1836)	*Oncorhynchus mykiss* Walbaum, 1792
Scaridium bosjani Daems & Dumont, 1974	*Scaridium longicaudum* (O.F. Müller, 1786)
Simocephalus gelidus Brady, 1918	*Daphnia gelida* (Brady, 1918)
Simocephalus intermedius Studer, 1878	*Daphniopsis studeri* Rühe, 1914
Stenhelia gracilis Brady, 1918	*Marionobiotus jeanneli* Chappuis, 1940
Thaslastrid sp.	*Marionobiotus jeanneli* Chappuis, 1940
Tigriopus brevicornis Giesbrecht, 1902	*Tigriopus angulatus* Lang, 1933
Tigriopus californicus Baker, 1912	*Tigriopus angulatus* Lang, 1933
Trichocerca relicta Donner, 1950	*Trichocerca obtusidens* Olofsson, 1918

AN IRREPLACEABILITY MAP FOR TASMANIAN PRIORITY PLANT SPECIES

by J.B. Kirkpatrick, O.Carter, F. Faulkner, L. Gilfedder and W. Potts

(with three text-figures)

Kirkpatrick, J.B., Carter, O., Faulkner, F., Gilfedder, L. & Potts, W. 2017 (6:xii): An irreplaceability map for Tasmanian priority plant species. 151: 59–63. ISSN: 0080–4703. Discipline of Geography and Spatial Sciences, School of Land and Food, University of Tasmania, Private Bag 78, GPO Hobart, Tasmania, Australia 7001 (JK*, LG): Department of Primary Industry, Parks, Water and Environment, Hobart, Tasmania, Australia 7000 (OC, FF, WP). *Author for correspondence: Email: J.Kirkpatrick@utas.edu.au

There is a strong need to map the relative importance of areas for nature conservation both inside and outside reserves, given increasing development pressures and ongoing threats to biodiversity. Nature conservation importance has typically been established using iterative or optimising systems which select areas to achieve explicit targets. Irreplaceability has been a concept used in many of these analyses. We calculated rarity-weighted richness values (irreplaceability scores) from reliable distributional data for all vascular plant species of conservation importance in one square kilometre grid cells covering the State of Tasmania, Australia. The spatial patterns of scores on the irreplaceability index were not strongly related to data collection intensity. Thus, our scores were reliable for most parts of the State, irrespective of survey effort, except where there were no or little survey data. Irreplaceability scores were high in places with concentrations of local endemics, on mountains with persistent snow cover, along the northern part of the coast and on the Bass Strait islands.

Key Words: irreplaceability, planning, plant species conservation, rarity-weighted richness, Tasmania.

INTRODUCTION

There is an ongoing need to identify conservation priorities, especially in the representativeness of elements of biodiversity in protected areas, but also to guide management decisions within existing reserves and development processes inside and outside reserves. Approaches to determine the relative importance of particular areas of land or sea for biotic conservation have been iterative (Kirkpatrick 1983), optimising (Kirkpatrick *et al.* 2007) or based on approaches to mathematical optimisation (Williams *et al.* 2004). The concept of irreplaceability, the degree to which an area cannot be replaced to achieve a target (Pressey *et al.* 1994), has been central to many of these approaches.

Algorithms incorporating the concept of irreplaceability have been widely used for reserve selection (Williams *et al.* 1996, Pressey & Taffs 2001, Cawardine *et al.* 2007, Linke *et al.* 2008, Cuesta *et al.* 2017). Irreplaceability measures have also been used to establish limits for offsetting (Bekessy *et al.* 2010, Brownlie *et al.* 2012, Gardner *et al.* 2013, Kiesecker *et al.* 2009, McKenney & Kiesecker 2010, Pilgrim *et al.* 2013), and, more recently, as a means of determining relative conservation value independent of tenure (Ma *et al.* 2016).

The general aim of biotic nature conservation is to maintain the diversity of life. However, the specific spatial targets that might achieve this general goal are difficult to determine. Therefore, there may be considerable virtue in measurement of relative importance for biotic conservation independent of specific spatial targets (Wilhere *et al.* 2008), despite the risk that poor reservation decisions could be made on the basis of the outcomes of this method alone (Segan *et al.* 2010).

Here, we use an irreplaceability index, based on the rarity-weighted richness of Williams *et al.* (1996), to indicate the spatial pattern of importance for plant species conservation in terrestrial Tasmania, Australia. We test the degree to which our results are influenced by collection intensity and how they relate to the areas revealed as important for conservation in previous prioritisation work.

METHODS

We used the Tasmanian Natural Values Atlas (NVA) (www.naturalvaluesatlas.tas.gov.au) to determine the number of recorded native vascular plant species and records of native vascular plant species for each 1 x 1 km grid placed over the terrestrial area of Tasmania, Australia. The NVA is curated and contains indicators of reliability and spatial specificity. We excluded unreliable records and those with a specificity of greater than one kilometre.

Numbers of species and records for native vascular plants listed as threatened under the Tasmanian *Threatened Species Protection Act 1995* or Australian *Environment Protection and Biodiversity Conservation Act 1999*, or that were otherwise uncommon, were also extracted from the NVA. These plant species are termed "priority plant species".

For each priority species, the number of 1 x 1 km grid cells that it occupied (I) was tallied. The irreplaceability index score for each grid cell was the sum of the inverse of I for all species, the rarity weighted richness of Williams *et al.* (1996). Thus, in a square containing two priority species, one confined to that square would score 1 (the maximum score) and another, present in 10 squares, would score 0.1. The summed score of these two species would be 1.1. We recognise that the distributional knowledge for our priority species is variable, but most of the score for any cell with high scores will derive from the highly localised species, which are the ones that are best known. Thus, the effect of these variations in knowledge on patterns will be low.

In order to test the effect of observation intensity on scores, Pearson's product moment correlation coefficient

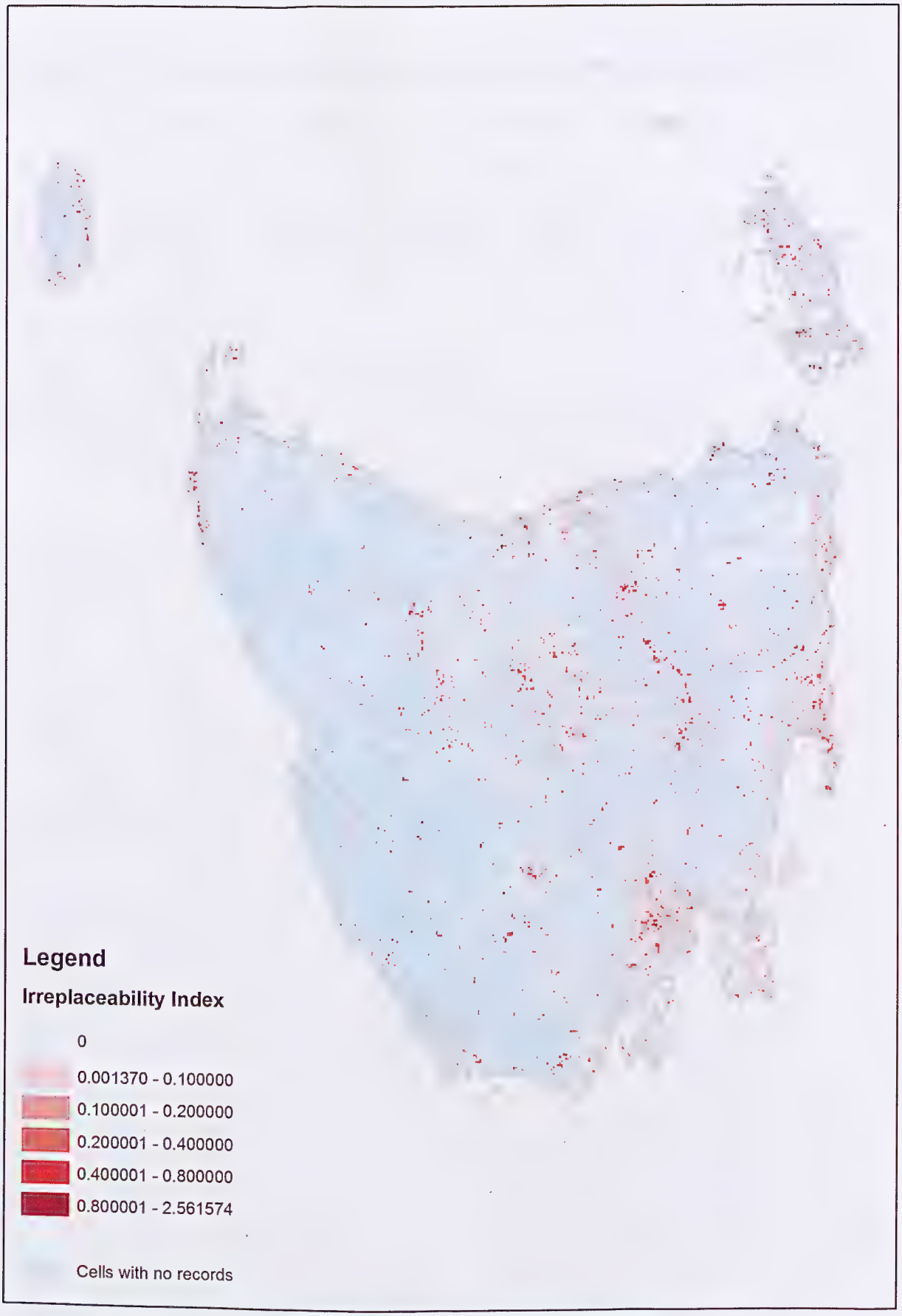

FIG. 1. — Patterns of irreplaceability for plant species for 1 x 1 km grid squares in Tasmania.

was used to determine whether the irreplaceability index was related to the number of non-priority plant species per grid cell or the number of non-priority plant records per grid cell. Grid cells with zero records of non-priority species were excluded from these correlation analyses. In order to gain an indication of the robustness of rarity weighted richness as an indicator of conservation importance, we compared the output of our index to the results of a past iterative approach. We used a Spearman's rank correlation coefficient on ranked cells scored using our irreplaceability index against the ranks of the places selected iteratively for representation of unreserved dicotyledonous plants in Kirkpatrick *et al.* (1991). Cells that were not selected in the 1991 paper were not included in the irreplaceability score column.

RESULTS

High irreplaceability index values were scattered, with occasional lineations and aggregations (fig. 1). There were high value grid cells in each of the centres of local endemism for plant species: the Asbestos Range, which contains many ultramafic endemics, the southern Midlands, containing semiarid country endemics, the eastern Central Plateau, containing alpine/subalpine endemics, the central east coast, containing dry forest endemics, the Tasman Peninsula, containing exposed headland endemics, the Hobart area, with endemics in a wide variety of environments, and the far south of southwest Tasmania with its alpine/subalpine endemics (Kirkpatrick & Brown 1984, Kirkpatrick 1999). There were sporadic high values in the northern Midlands, along the northern coasts and on the Bass Strait islands. These were concentrations of species whose distribution included mainland Australia, but extended to northern Tasmania. The places in Tasmania with the most persistent snow cover, including Ben Lomond, Mount Field, Mt Anne, Frenchmans Cap and the Du Cane Range, had high irreplaceability values, largely attributable to species that are restricted to habitats with persistent snow, but which are more common in mainland Australia or New Zealand, where there are more extensive areas with persistent snow (Kirkpatrick 1997, Parry *et al.* 2016).

Collection intensity had little effect on irreplaceability scores. Significant ($P < 0.001$) correlations between the index, species, and records, were found, but had an extremely low level of explanation ($r^2 = 9.7\%$ for species and 3.8% for records). Grid squares with high irreplaceability scores had few or many records of non-priority species, and few or many non-priority species (figs 2 and 3).

The rank order of plant irreplaceability scores was weakly positively related to the order of selection of places for unreserved plant species by Kirkpatrick *et al.* (1991) ($r = 0.291$, df = 68, $P = 0.015$).

DISCUSSION

Our test of the relationship between the iterative ranking of areas for unreserved dicotyledonous plants in 1991 and ranking of our irreplaceability scores was biased against a positive result by the inclusion of reserved species, monocotyledonous plants and pteridophytes in the latter data set and the quarter century available to accumulate further records. The positive correlation reflects the robustness of both techniques in determining relative value.

Although the magnitudes of irreplaceability scores reflect priorities derived from methods designed to approach or achieve optimisation in relation to targets, target-based approaches to optimisation will be more efficient in selecting reserves (Albuquerque & Beier 2015). With irreplaceability scores, there is no certainty of the value that will include all target species at a defined target level. Nevertheless, irreplaceability scores should give a strong indication of prospective localities for reserves, and be more stable in their patterns than optimisation selections, which shift when reservation is achieved to target for some of the elements targeted. The latter consideration is particularly important when determining whether there would be problems with impacts on priority species as a result of proposed developments within existing reserves.

Our irreplaceability index is designed to provide a first indication of conservation significance for vascular plants in development assessments and environmental management plans. A layer, *Distinctiveness of Areas of Threatened and Uncommon Plants*, derived from our approach is available for such conservation planning on the Department of Primary Industries, Parks, Water & Environment's Conservation Information System (www.dpipwe.tas.gov.au/cis).

Although strong patterns are evident in figure 1, users of the output spatial layer should not rely on low irreplaceability index scores, especially where the number of records of all vascular plant species is zero to low, because low values are highly likely to indicate lack of survey effort. The linear patterning of high value cells in some parts of the State (fig. 1) indicates sampling along roadsides, but not in adjacent country, rather than the reality on the ground. The cells with a value of zero are those with very few records overall (fig. 3), and for most cells there are no records at all (fig. 1).

It may be possible to remotely estimate the irreplaceability index from environmental and land use surfaces, using methods such as the deep cognitive imaging systems applied to predict fire incidence from climate data (Dutta *et al.* 2013). However, any such predictions should be validated by field checking for any development assessments.

The irreplaceability mapping process can be extended more widely, both taxonomically and in space. For example, short-distance-dispersing and territorial fauna, critical habitats for other faunal species, elements of geodiversity, vegetation types and land systems are some of the potential inputs for which data layers exist. The approach can be applied anywhere there are spatial data

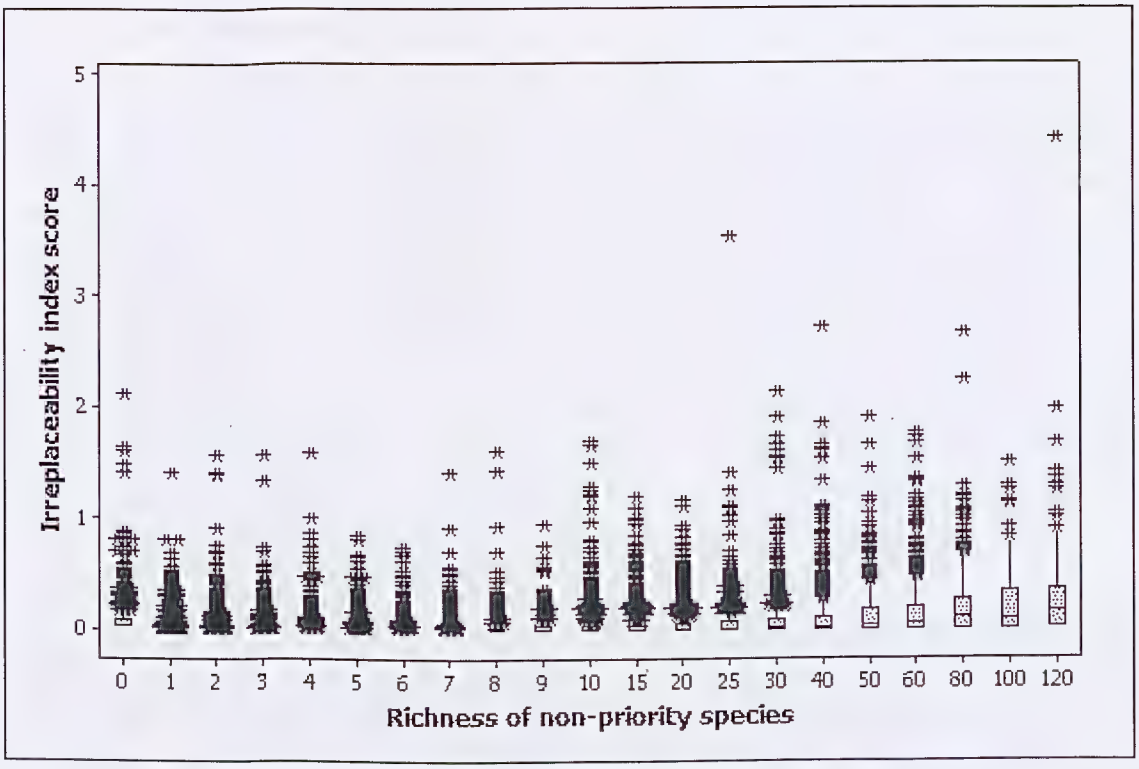

FIG. 2. — Box plots showing the relationship between the irreplaceability index and the number of non-priority species in 1 x 1 km grid squares. One quarter of the values in any class are shown as a vertical line and asterisks representing individual 1 x 1 km grid cells. 10 = 10–14, 15 = 15–19, 20 = 20–24, 25 = 25–29, 30 = 30–39, 40 = 40–49, 50 = 50–59, 60 = 60–79, 80 = 80–99, 100 = 100–119, 120 = > 119.

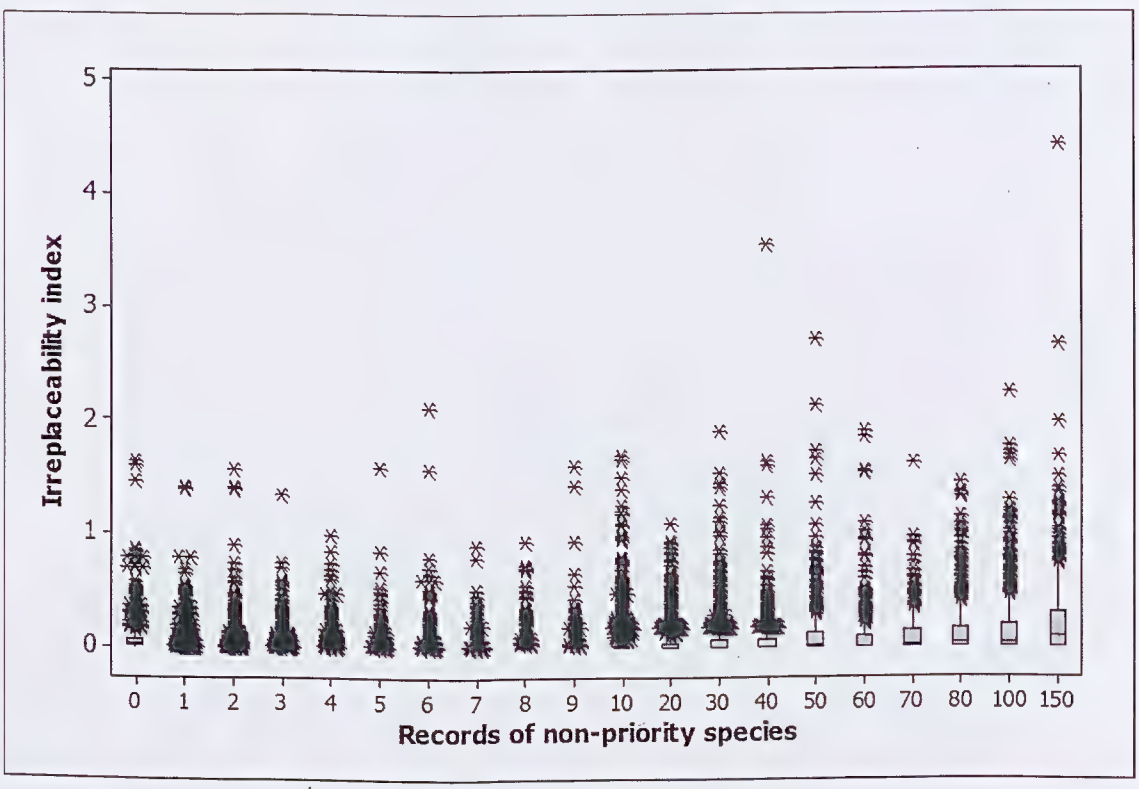

FIG. 3. — Box plots showing the relationship between the irreplaceability index and the number of records of non-priority species in 1 x 1 km grid squares. One quarter of the values in any class are shown as a vertical line and asterisks representing individual 1 x 1 km grid cells. 10 = 10–19, 20 = 20–29, 30 = 30–39, 40 = 40–49, 50 = 50–59, 60 = 60–69, 70 = 70–79, 80 = 80–99, 100 = 100–149, 150 = > 149.

on elements of nature, and at any scale. The approach is independent of any target, rather than responding to proportionate representation.

ACKNOWLEDGEMENTS

We thank the Department of Primary Industries, Parks, Water & Environment for the use of plant species records from the Natural Values Atlas.

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(accepted 7 November 2017)

THE SINISTER STEEPLES OF ALEXANDER NORTH

by Eric Ratcliff

(with 15 plates)

Ratcliff, E. 2017 (6:xii): The sinister steeples of Alexander North. *Papers and Proceedings of the Royal Society of Tasmania* 151: 65–78. ISSN 0080-4703. Albion House, 153–155 George Street, Launceston, Tasmania 7250, Australia. Email: eric.ratcliff.albion@gmail.com

Alexander North (1858–1945), who practised chiefly in Tasmania, was an outstandingly original architect during the stylistic period in Australia now commonly called Federation. His work includes features that represent an extreme expression of established forms, and draws attention to some inadequately explained characteristics of the period. Prominent among these is a series of church spires that North designed in Tasmania between 1893 and 1927, which evoke peculiar associations in the minds of many who notice them. Those associations, which depend mainly on graphic works published during the same era, were unlikely to have been intended by the architect. They provide evidence in support of an associationist theory of aesthetic response that has gone out of fashion, and a salutary reminder that architectural historians must seek to see through the eyes of their period and not the projections of hindsight.
Key Words: Alexander North, architecture, Federation styles, aesthetics, associationism.

INTRODUCTION

For an architectural historian, a particular interest is in why buildings look as they do, and that inevitably leads to questions of social history, geography, geology, economics, theology, aesthetics and even politics. Beyond questions of who did what, when and where, there is the mysterious, and frequently unanswerable, question of why? In approaching that, we can consider why, generations after the event and in a world of different presuppositions, we are likely to get it wrong.

In 2011 Foot and Playsted, the important Launceston printing and publishing firm, gave their graphic designers the task of producing a striking set of images of buildings in the city for their coming year's calendar. One of the results is a tenebrous drawing of the east end of Holy Trinity Church standing tall against a leafless tree and a lowering sky, the belfry and spire rendered in atmospheric detail, and a bird of ill omen flying away as if in fear.

Ravens have been considered harbingers of death, pestilence and ill fortune since ancient times. In the etchings of Charles Meryon, they appear in association with images of Gothic buildings, ever more intrusive as the artist's insanity advanced. His most familiar image, *Le Stryge* (1853), is of a devilish figure brooding over Paris from a tower of Notre Dame, with the birds circling the distant Tour Saint-Jacques and approaching to emerge beyond the picture-plane, menacing the viewer. In later etchings filled with foreboding, they wheel around the towers of the great cathedral and sweep in a flock to shadow the Left Bank, or fill the sky above the Seine. Since then, if not before, the association between the architectural Gothic and the bird of ill omen has become an iconographic cliché, part of the imagery of a popular fashion that has usurped the name of the architectural style. Its reappearance in contemporary Tasmania appears to have been evoked by the presence of a church surmounted by a most peculiar steeple, the most elaborate of a series designed by Alexander North, arguably the most important architect ever to practise in Tasmania. Why should a feature of his most admired building produce such a response in a later generation?

The work of Alexander North has yet to find the recognition it deserves. This is largely the result of geographical location, although his most celebrated building is the chapel of Trinity College within the University of Melbourne, and others appeared in South Australia, New Zealand and even in Fiji. Most of his work was in Tasmania where much of it can still be seen, but some of his most major projects did not achieve completion. Anyone in quest of North must rely greatly on the lifelong researches of the Melbourne historian, John Maidment, whose definitive publication on his hero has been long awaited, although he has been extraordinarily generous in sharing the findings from his work in progress (Maidment 1981, 1982, 1988). Maidment has stated that "North worked on designs for more than 200 buildings during his Australian career" (Maidment 2012, p. 504). North also figures in Caroline Miley's work on the Arts and Crafts Movement in Tasmania (Miley 1987), and the disappearing memories of those who knew him.

ALEXANDER NORTH (1858–1945)

North was born in 1858 in Huddersfield in the West Riding of Yorkshire, the son of a linen-draper. After leaving school, he was articled to an architect at Kendal in Westmoreland, and attended the School of Art there before moving to London where in 1876 he was working in the office of James Cubitt (1836–1912) and attending the Lambeth School of Art. As an articled draughtsman and a young architect, Alexander North travelled extensively on the Continent, and his later work was clearly influenced, whether by direct experience or through his publications, by the great French restorer and architectural theorist, Eugène-Emmanuel Viollet-le-Duc (1814–1879).

James Cubitt was not a member of the famous family of engineers and builders of the same name; he was the

son of a Baptist minister from Norfolk who became a notable designer of Non-conformist chapels and wrote an influential treatise on *Church Design for Congregations* (Cubitt 1870). In that and other works he argued against the revival of mediæval compartmentation, the separation of nave, aisles and chancel, and the elongation and division of the congregational space. He complained that strong columns obstruct both sight and sound and slim columns are aesthetically unsatisfactory (Cubitt 1870, 1884, 1892).

While working for Cubitt, North prepared drawings for the Union Chapel in Compton Terrace, Islington. This building has a spacious octangular auditorium fronted by a bold square tower of red brick and contrasting stone, topped by an exiguous belfry and spire. This feature was noticed by Nikolaus Pevsner:

> *The external effect (and what a blustering High Victorian effect) is the big red brick tower crowned by an odd spirelet, breaking with the Georgian restraint of Compton Terrace.* (Pevsner 1952, p. 230)

The "odd spirelet" is an octangular belfry topped by a slated spire, mounted on the ridge of the gabled roof to the tower. The sloping timbers of the belfry are continuous with those of the spire, which is slightly flared at the bottom, a form that Alexander North was to use repeatedly in Tasmania, but with a wider flare, and arguably with a greater flair.

Cubitt's spacious preaching-houses clearly had their effect on the designs of the more liturgically-minded Alexander North; St John's and Holy Trinity in Launceston are both notable for the breadth of their congregational spaces, despite their traditional cruciform plans. An experience of the interiors of these two churches should be compared with those of Gothic Revival buildings based on the mediævalising principles of A.W.N. Pugin, like the Church of the Apostles in Launceston and the two cathedrals in Hobart.

In 1883 North was awarded a gold medal in Britain's National Competition for students of Schools of Art for original "cathedral drawings" (*Launceston Examiner* 1886). For some decades, British architects had been busily producing designs for Anglican cathedrals for the colonies, and North's competition entry was of this genre. The plan includes the wide congregational space enjoined by Cubitt, and resembles that eventually achieved at St John's in Launceston. In the same year, for reasons of health, North took ship for Australia, and arrived in Hobart late in the winter. In November he started work in the drawing office of the Department of Lands and Works, and his first major project was the Launceston Post Office, designed in what was described at the time as "Queen Anne" style, and opened in 1886, the year he left the government service.

While supervising the building of the Post Office, North recognised the opportunities to be found in Launceston at the time, for it was undergoing a minor boom, driven principally by mining, substantially capitalised, managed and equipped from the city: tin from Mount Bischoff and the North-East, smelted in the city, and gold from Beaconsfield, Lefroy and Mangana. The moneyed citizens of Hobart were well supplied with early colonial houses and later mansions designed by Henry Hunter and others, but in Launceston, there was a demand for houses to display the new wealth.

North's government appointment allowed a right of private practice, and he worked for a time in association with Leslie Corrie, who practised in Launceston before following his former master, Henry Hunter, to Brisbane in 1886. The first Gothic Revival design for the rebuilding of St John's Church, Launceston, was attributed to the partnership of Corrie and North, and Corrie was responsible for the 1884 design of the Catholic Church of the Holy Redeemer at Deloraine.

The work of North and his partners spanned the years when the city gained a remarkable heritage of buildings in "Federation Queen Anne" and related styles, designed by Thomas Searell, J. Martyn Haenke, Thomas Tandy the elder, Alfred E. Luttrell, A. Harold Masters, and others. Remaining city buildings from that era range in size from a once grand hotel to a former gentlemen's public lavatory, and even to a South African War memorial. North and his partners designed secular buildings in and near the city, but as a devout member of the Church of England, he was much in demand as an ecclesiastical architect, and he also designed for other denominations. He is best known locally for his two great unfinished Anglican churches, St John's and Holy Trinity, as well as two other parish churches within the city limits.

North was interested in botany, and in the promotion of Tasmanian timbers for export (North 1891, 1904) and he became a respected pillar of the local Arts and Crafts Movement (Miley 1987). His designs include traditional Gothic vegetable motifs, but his interest in native plants flowered in his Art Nouveau-influenced designs for capitals in the 1938 nave arcade of St John's, Launceston, exquisitely carved in wet concrete by Gordon Cumming (1894–1972).

North's partner in Launceston during many of the years before the Great War was the remarkable A. Harold Masters, a pioneer in the technology of electricity, radio telephony, X-ray photography and concrete construction (Masters 1900, Proverbs 1988, Neale 2012). Masters built his own house of "camerated concrete" as early as 1902, and was involved with North in the 1911 design of St Margaret's Hospital for the celebrated surgeon who became Sir John Ramsay, as well as other constructions in a material relatively new to architects, although long-established in engineering and industrial use (Morris-Nunn 1989, Ratcliff & Ratcliff 2005). Concrete was used to construct North's unique dome and pendentives over the crossing at St John's and the grain silos at Ritchie's Mill, both in 1911, and Masters's grandstand at Mowbray Racecourse in 1914 (Green 2006).

North's work for the Church of England in Tasmania also includes St Michael and All Angels at Bothwell and many lesser churches, but the present essay will be limited to those that carry the varied members of a family of steeples that appear strangely sinister to many viewers of those that remain today.

A MYSTERIOUS CHANGE OF CHARACTER

Architectural history is dominated by notions of style, but the experience of buildings for most people is more likely to be coloured by less tangible qualities that are best described in terms of *character*. Buildings are described as humble or stately, imposing or unassuming, spectacular or unsightly, plain or ornate, handsome or elegant, cosy or frivolous, welcoming, or forbidding; some may be experienced as sinister, or in popular parlance, spooky.

In the last decade of the nineteenth century and the Edwardian decade, a peculiar change in aesthetic sensibility became widespread throughout the British Empire. It was not without parallels on the Continent and in the United States, but the particular British manifestations of it belong to our present subject. In the decorative arts, the advanced styles included what are now commonly identified with Art Nouveau, the Aesthetic Movement and the Arts and Crafts Movement. In architecture there was also Edwardian Baroque, Queen Anne Revival, Tudor Revival, a free style that embraced motifs from some or all of these, and an increasing North American influence; all of these are represented in Tasmania.

Although these styles show obvious differences, most of them share a quality that might be described in terms of emphasis and excess. These may be expressed in the sinuous lines of Art Nouveau that startled a world accustomed to simple geometry, Classical restraint or Gothic seriousness, or else the exaggerations of scale in Edwardian Baroque, or the complicated roof-forms, vivid colour contrasts, and multiplicity of surface materials characteristic of the revived "Tudor" and "Queen Anne". It was in the free conjunction of styles around the turn of the nineteenth century that the most emphatic departures occurred. Familiar examples include the exaggerated verticality in Charles Rennie Mackintosh's designs, more apparent in his furniture than his architecture, and the heavily simplified features and overhanging hoods above doorways in the work of Charles Francis Annesley Voysey.

Many of the leading English architects of the new generation that marched into the twentieth century had served their time under the great men of the later Gothic Revival, some of them veterans of a "battle of the styles" alleged to have been waged in the mid-Victorian period. It is a recurring tendency of youth to seek ideological purity, and judging from their mature works, many articled draftsmen towards the end of the nineteenth century appear to have expressed this in a search for a synthesis and a style that would be both "national" and in tune with the times. Whether or not that was ever achieved before the field was overtaken by "international" modernism is still a subject of some interest (Crook 1987).

These articled draughtsmen had become accustomed to the vertical emphasis of Gothic, and this survived their youthful rebellion, but the spirit of the age was, for reasons that remain mysterious, against carrying the eye of the viewer into the sky by means of pinnacles, and from the ghost of the Classical tradition came horizontal features to put a stop to that (pl. 1). Some have retrospectively

PLATE 1 — A. Harold Masters: mortar-board finial, Barratt's Music Store, Launceston.

seen this as symbolising the ending of the last great "age of faith", or a premonition of the disasters to come in the twentieth century; buildings could no longer point to heaven, but they might be needed to hold up the sky. In the design of all buildings above the ground, there is a tension between the vertical and the horizontal, but one of the recurring characteristics of Edwardian architecture in all its styles is a particularly emphatic expression of that tension. Victorian building was characteristically heavy on the ground, but usually aspired towards the heavens. Suddenly, in the last decade of the century, the most innovative architects began to deny that.

Some manifestations of this are frequent and familiar in Tasmanian buildings of the period. For several generations, internal architraves had most commonly consisted of a series of mouldings around the opening, usually continuous and mitred at the corners. Suddenly, the mouldings became simpler or disappeared entirely, and at the top was placed a horizontal cornice like a narrow shelf. Furniture designs reflected the change even more emphatically; finials on vertical timbers either disappeared or gave place to flat-topped elements. When features like these appear on a larger scale on the outside of buildings, they remind us of Lewis Carroll's parodic "tea-tray in the sky", particularly when they are finials. The little domestic towers, the chimney-tops, had long been given mouldings near the top, but these suddenly became thinner and wider in the hands of some designers, and the Tasmanian architectural practice that is examined in this essay took them to an

ultimate extreme, a particularly emphatic expression of the apparent shift in aesthetic sensibility (pl. 2).

The Australian colonies that became states of the Commonwealth in 1901 also had architects in search of a style that might express the spirit of the age, and in the writings of a few (but not conspicuously in their buildings) there were expressions of a wish to develop a national style. It has also been argued that the national aspirations of the majority were as much inclined towards Imperial solidarity as to Australian patriotism, and even to an Anglo-Saxon racial sentiment (Willis & Goad 2008). Their houses, like the bungalows of British India, were devised to shelter an essentially British way of life, but with external appearance dictated chiefly by economics and climate, and therefore a strong contribution from the colonial traditions of the large exposed roof and the surrounding verandah.

This is not the place to argue for or against the stylistic term "Federation" that rapidly prevailed in Australia after it was first proposed by the art and architectural historians Bernard Smith and David Saunders, and is now so beloved of real estate agents and developers (Smith 1969, Saunders 1969). It has been argued that the styles, at least in their domestic manifestations, are characteristically Australian, and there has been attributed to them a nationalistic motivation, a projection that relies chiefly on the coincidence of the years of their development with those of the political movements that led to Federation (O'Neil 2000). A national motive can be discerned in the appearance of terracotta kangaroos in place of French dragons as finials upon Marseilles-tiled gables and the representation of native fauna and flora in lead-lighted windows, but in little else. Most of the architects involved were British-trained if not British-born, and the external appearance of their houses was a characteristic response to antipodean requirements and conditions, enclosing interiors essentially identical with their English contemporaries. Eucalyptus hardwood was fumed with ammonia to darken it, and given the trade name of "Tasmanian oak", a persisting term that smacks more of "cultural cringe" than of nascent nationalism.

PLATE 2 — A. Harold Masters & Alexander North: house in Elphin Road, Newstead.

The "tea-trays in the sky" had made their first prominent appearance indoors, in miniature, and in London. In 1884 Arthur Heygate Macmurdo, one of the founders of the Century Guild, an important association in the development of the Arts and Crafts Movement, designed an exhibition display consisting of a furnished room with two walls replaced by thin colonnades to allow the interior to be viewed (Pevsner 1936, 1968) (pl. 3). The square posts were given excessively wide capitals and supported a broad shallow cornice, and above that was a series of panels separated by slim piers that ended in most peculiar finials: flat square "trays" or "mortar-boards" that stopped the rise of the gaze with a sudden jerk. The room was exhibited again in Liverpool in 1886, and a magazine illustration of its appearance there started a fashion that spread even to these far Antipodes.

The motif was applied by North's now celebrated contemporary in England, C.F.A. Voysey (1857–1841), and in the first decade of the new century his designs for furniture and buildings were illustrated in periodicals such as *The Studio,* read in the colonies by people who wanted the latest from Europe. Downmarket versions appeared in the catalogues of such firms as Foy and Gibsons in Melbourne and Coogans in Tasmania (Coogan 1913, Foy 1923). The vertical members of chairs, bedsteads and chimney-pieces and any other items that could be made to project above the horizontal were capped with little square finials.

The much larger versions that appeared atop the piers and parapets of buildings in Launceston emerged particularly from the office of Alexander North and Harold Masters. North does not seem to have been content to stop at the horizontal feature, and some bizarre embellishments are attributable to him. In 1907 McKay, Sampson and McKinlay's department store in Brisbane Street was destroyed by fire, and the front of North's very up-to-date replacement did not finally culminate in Macmurdo finials; those at the ends support large balls on Art Nouveau legs (pl. 4). Even more outrageous finials topped the belated Art Nouveau verandah added to the plain Georgian Berriedale Inn at Westbury, across the road from North's completion of the tower of Henry Hunter's Holy Trinity Catholic Church. North was no conserver of early colonial architecture; three of his churches involve alterations and additions to existing buildings in ways that entirely change their character, and that was also the case at Westbury. Plainer but more emphatic examples of the mortar-board finial were applied to buildings that can be attributed to his partner, Harold Masters.

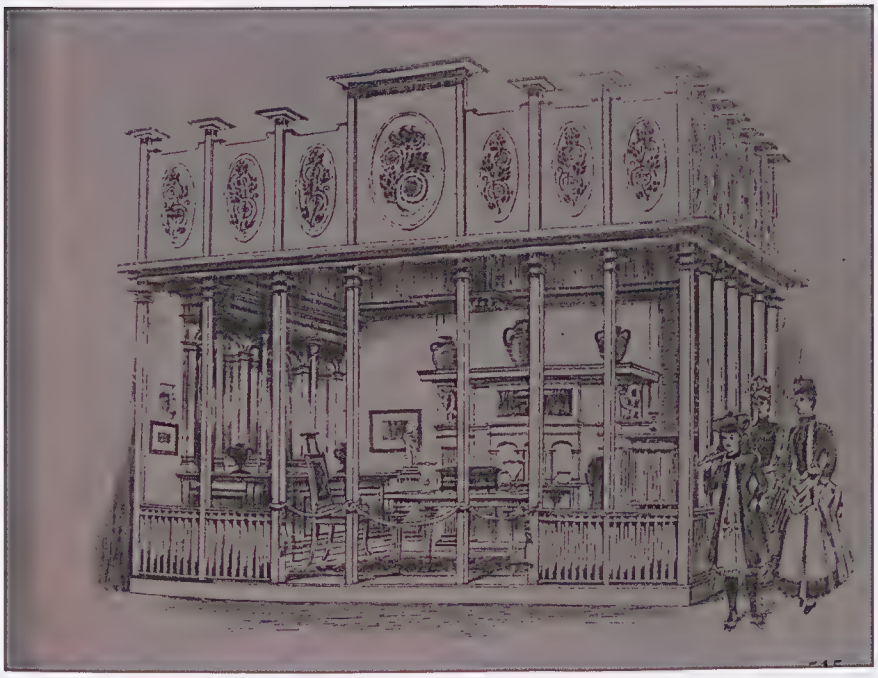

PLATE 3 — Arthur Heygate Mackmurdo: Century Guild Stand, Liverpool International Exhibition 1886.

At No. 79 Elphin Road, Launceston, is a house that has some of the red brick and Gothic of North, and some of the freestyle concrete of Masters. Its chimneys carry cornices even more emphatic than Barratt's finials. In about 1910, North or one of his associates designed the Newstead Hotel, a replacement for one of the few suburban hostelries in the city. It is still a handsome building, despite the commercial mutilations that appear to be inevitable to its trade. High above the roof there can still be seen what may be in proportion the widest and shallowest cornices ever to appear on an Edwardian chimney-stack (pl. 5). They are about two and a quarter times as wide as the supporting shaft, and were probably achievable only through Harold Masters' mastery of

PLATE 4 — Alexander North: orb finial, former McKinlay store, Launceston.

PLATE 5. — A. Harold Masters: chimney-stack, Newstead Hotel, Launceston.

concrete. The cornices are just that extra bit wider and slimmer than any of the others in the city, if not in all of Australasia. They would not have been easy to make, and the exaggeration was clearly deliberate, a minor apotheosis of the prevailing fashion.

The derivatives of Macmurdo's "tea-trays" might arrest the rise of the gaze above commercial façades or domestic chimneys, but Alexander North was not one to stop the reach of his churches towards Heaven. He did, however, express the horizontal spirit of his age even in his steeples, and the results of that are now to be examined more closely.

OF STEEPLES AND SPIRES, AND CHANGES OF PITCH

It is necessary here to introduce a note on nomenclature, to avoid confusion. Steeples and spires are not quite the same thing. The term "steeple" is mainly held to imply a church tower, whether crowned with a spire or not. Early English and American Quakers and some other non-conformists called places of worship "steeple-houses", for a church was for them a body of believers and not a building, and in the sixteenth century, the term "spire-steeple" was used to distinguish a tower topped with a spire.

Spires on churches are an invention of the middle ages, a deliberately spectacular exaggeration of the conical or pyramidal roof required for a tower. We readily associate their tall pointed forms with Gothic, but they originated near the time when the later builders of the Romanesque had just begun to recognise the advantages of the pointed arch, both in structure and in the architectural expression of the meaning of a building. One of the earliest that can be closely dated is the still incomparable one on the south tower of the cathedral at Chartres, completed in 1165, just eleven years after the completion of Abbé Suger's innovation at St Denis that is considered to be the first major essay in Gothic.

In the middle ages, spires were more often an aspiration than an achievement; even the cathedral at Chartres was intended to have nine and has but two, and the cathedrals of Paris and Rheims had none until Viollet-le-Duc added his ornate *fleche* above the crossing in Paris in the nineteenth century. Melbourne has two cathedrals each with three spires, a phenomenon unknown in any city in Europe! Smaller mediæval churches were generally provided with a tower, not merely to house a bell, but also in some cases to accommodate the priest. These were topped with spires whenever they could be afforded. England and Ireland have many spires; in Scotland they appear also on secular buildings, and they are entirely familiar in these antipodes, but nowhere are they more prevalent than in France.

The visual transition from a square tower to a pointed spire can be accomplished in five ways. The simplest, generally found in Germany, is the steepened pyramid; the others require some architectural device to make the transition visually satisfactory. The belfry stage of the tower could be made octangular, with sloped set-offs at the corners, as in Henry Hunter's towers at All Saints in South Hobart and St John's at Ross, and in William Henry Clayton's work at St Andrew's in Launceston and St Mark's at Deloraine. Subordinate pinnacles could be placed on the corners of the tower; this can be seen *in excelsis* on Salisbury Cathedral in England, where little spires gather at the foot of their mother. In simpler form, it explains the pinnacles on the now spireless tower of the church at Port Arthur. Another expedient is the broach spire, where the corners are given little pyramid-like structures that lean into four facets of the octangular spire. These can be seen in Hubert Springford East's splendid addition to St Mary's Church at Hagley, made in 1932. North chose the fourth expedient, the splay-foot spire, in which the steeper part emerges from a less precipitous roof that overrides the walls of the tower. The architectural advantage of this is that the steeper section can have any number of sides, four, six, eight, or even more, unlike the other forms, limited to four or eight. The economic advantage is that a spectacular result can be achieved with relatively cheap materials.

Between 1889 and 1901, a belfry and steeple were built to straddle the ridge over the crossing of the new Holy Trinity Church in Launceston (pl. 6). The building, North's unfinished masterpiece, combines red brick and mustard-coloured sandstone in a *fin-de-siecle* Gothic that is in debt to many sources, yet highly original. It was intended to have an uninterrupted roof extending over nave, crossing and chancel, with lower transepts enlivened with semicircular appendages, a clergy vestry with a conical

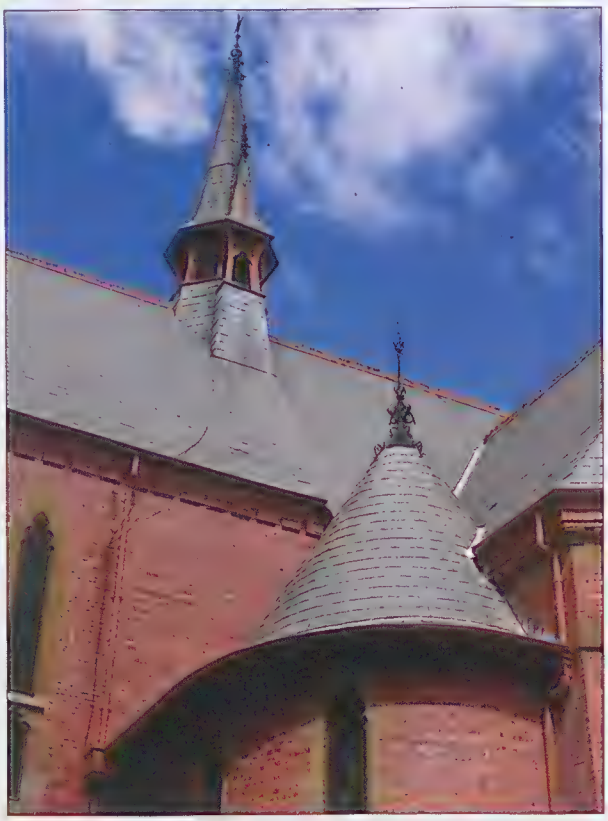

Plate 6. — Alexander North: Holy Trinity, Launceston, belfry, *fleche* and north transept chapel.

roof on the south side and an apsidal chapel to the east of the north transept. The exterior of the latter makes North's debt to the great French architect and restorer, Eugène-Emmanuel Viollet-le-Duc, very clear. The *Dictionnaire raisonné de l'architecture française du XIe au XVIe siècle* was published from 1858 and completed in 1875, and the illustrations if not the text had a profound influence on the last phase of the Gothic Revival in England, the time when Alexander North was articled. The conical slate roof on the chapel at Holy Trinity shows the change of pitch that Viollet-le-Duc used to such striking effect on such works as the bastions at Carcassonne or the towers of the Chateau de Pierrefonds in Picardie – powerful reinstatements rather than restorations (pl. 7).

The shallowing of the roof pitch just above the eaves is characteristic of parts of Europe with a high snowfall, and for this and unrelated reasons was a regional characteristic that became widespread in France during the nineteenth century, so much so that it imparts a Gallic air to almost any building it is applied to (pl. 8). Some of the lithographers making prints after the drawings of the artists attached to the French expeditions that visited Van Diemen's Land in the early decades of settlement show our colonial cottages with roofs of similar form, which they did not generally have. They make it possible to imagine what the settlement at Sullivans Cove might have looked like if the French had settled there first.

The form is made possible by the use of a little subsidiary rafter, in English described as a *sprocket* and in French a *coyau* (Lavenu & Mataouchek 1999). Viollet-le-Duc used *coyaux* to give his conical roofs a Gallic frisson with varying degrees of emphasis, some with narrow eaves and a few almost as wide as Alexander North's. The form is thought to have two independent origins: in regions subject to frequent snowfall, it was probably intended to throw snow sliding from a steep roof clear of the walls; in Languedoc, it may have originated in structure to support the eaves of a thatched roof, the shape being hidden under a thick layer of thatch until revealed by its replacement with a covering of tiles or slates (Donald 1995). Its structural advantage in a steeple is that the principal timbers can rest directly on the walls.

The flare above the eaves can be applied to a pitched roof of any form, but when it is applied to a spire, it becomes an emphatic feature. Alexander North added further emphasis, creating a strong visual feature as well as a way of keeping the water out of the walls, but the exaggeration results in a complete change of character. In his ridge-mounted spires, with the main structural timbers appearing below them as the leaning pillars of the belfry, he used the flare to visually separate the one from the other, another expression by North of that horizontal emphasis characteristic of an era more imperial than pious.

Plate 7. — Eugène-Emmanuel Viollet-le-Duc: detail of watercolour of scheme for restoration of Tour de la Vade, Carcassonne, 1853.

Plate 8 — House at Vernonnet, Normandy. The *coyeau* form of the roof probably reflects replacement of thatch with tiles.

SINISTER STEEPLES

North applied the splay-foot form in a number of different ways, some much taller than they are wide, some wider than they are tall. The spire may be square, hexangular, octangular or more complex in plan, and it may be clad with slates or sheet metal. In their emphatic form they have no significant precedent in English church-building, even during the late nineteenth century, but a little more in France.

The earliest of Alexander North's sinister Anglican steeples in Tasmania is at Nile, south of Evandale. In 1850 a plain red brick schoolroom had been built in the hamlet, then known as Lymington. In the following year it was dedicated for use as a church, and in 1893 was made to look like one by Alexander North who altered the side windows and added a chancel, a vestry, a tower and buttresses, before the building was consecrated as St Peter's Church, Nile (pl. 9). The additions were in Alexander North's favoured red Sandhill brickwork, with hood-mouldings of moulded special bricks and foliated terracotta castings at the drips. The sloping buttresses of the tower create a false perspective that makes it appear taller than it is, and it is crowned with a hexangular spire emerging from a wide pyramidal roof with a slope of about 30 degrees and overhanging eaves. The spire and roof are clad with rugged grey slate like the scales of a *Trachysaurus* lizard, varied with a band of slates with pointed tails. The light colour and attractive irregularity of the slates makes it highly likely that they are of Tasmanian origin, probably from the newly-opened quarries to the east of the Tamar Valley at Bangor or Turquoise Bluff. Seen from the front, the paired pointed openings of the belfry stare down at the viewer from under hood mouldings, greatly increasing the impression created by the reptilian hat.

Plate 9 — St Peter's, Nile, brick tower and slate-covered spire.

The much more elaborate *fleche* at Holy Trinity, Launceston, that gave rise to this essay was next in order of construction. The building was designed by 1898, and the spire was in place by the time of its consecration in 1902 (Branagan 1989, Gill 2010). The spire is clad with slates, and is mounted on the ridge of the roof above the centre of the crossing. It has subsidiary wings on both sides with roofs that descend to a lower level than that of the spire. The roofs are flared at the bottom and shelter an open belfry whose sloping timbers are continuous with those supporting the spire and the wings. Cusped spandrels in the belfry and wrought iron finials provide the elaboration necessary to harmonise with a complex form.

In 1903 a small weatherboarded church was built for the railway village of Parattah in the Eastern Midlands. North designed St George's with a louvred belfry and small spire, square in plan and mounted diagonally on the ridge of the roof, but this was elaborated into the hexangular structure that stands today, the metal-clad spire being flared at the bottom to throw water clear of the belfry, and to provide a visual separation. The posts of the belfry continue upwards as supports of the spire.

North must have become exceedingly familiar with the railway journey between Launceston and Hobart, for in 1907 he was supervising the rebuilding of the chancel of St David's Cathedral in Hobart; the previous work carried out under the supervision of George Fagg in succession to Henry Hunter had had to be taken down because of foundation problems. He is thought to have visited England and consulted G.F. Bodley, the designer of the cathedral, but it is not certain that they met as Bodley died later in the same year (Boyce 2012). North's other major Anglican project in Hobart was the cloistered wing added to the old Hutchins School in Macquarie Street, opened in 1914.

Edward Dumaresq built a schoolroom of rubble bluestone and brick on a hilltop on his property at *Illawarra* on the edge of the Norfolk Plains in 1841–1842. As at Nile, the schoolroom doubled as a chapel-of-ease, dedicated as Christ Church, like the mother church at Longford, and a chancel was added in 1888. In 1905 Alexander North designed a new chancel and transepts, an Arts-and-Crafts Gothic porch, and a squat tower over the crossing (pl. 10). This is crowned with the broadest of his characteristic spires, clad with sheet metal. The splay foot is square in plan, with a gentle catenary curve, its broad eaves supported by curved corner brackets. The perfectly proportioned peak is octangular. A plain rural building with an excellent site has become a cruciform landmark that seems entirely at home on its hilltop, for North has avoided the spectacular and harmonised his steeple with the breadth of the tower the shape of the hill and the low pitch of the old schoolhouse roof.

North's next commission was for a spacious weatherboarded Holy Trinity Church of England at Beaconsfield; its predecessor had become too small for the busy gold town by 1907. North responded to its unremarkable corner site by placing a square tower at the corner. The boom went bust, and the belfry and spire were not completed until 1925; the latter, clad with sheet metal, followed on a smaller scale the form he used at Illawarra, except that the steep part is four-sided. Although not the first to be executed, this was the first of North's designs for a square tower topped by a louvred belfry of similar breadth and a metal-clad spire that looks as broad as it is high.

The finest of his metal-clad spires was raised in another gold-mining town, Mangana near Fingal, in 1910 (Andrews 2001) (pl. 11). This outstanding little church for a Catholic congregation was built of concrete, the surfaces not rendered but displaying evidence of excellent form-work, and green and brown glazed earthenware tiles are inset flush with the surface to stand for architectural decoration. The entrance porch is the lowest stage of the tower. Our Lady of the Sacred Heart would be a gem in any landscape; it is durable, practical, innovative, quirky, and beautiful, and as always, the metal-clad spire is perfectly harmonised with the hilly surroundings. The grey concrete is now painted white, but without detriment to the overall effect of a remarkable building.

A more economical version was built at Lachlan near New Norfolk in 1911, to replace a chapel-schoolroom destroyed by fire (Henslowe 1978). The former St George's is of timber clad with roughcast render, and the tower and belfry have been given sloping sides to create an illusion of solidity and height. The tower contained the vestry, and above the open belfry, a square witch's hat covered with sheet metal extends over wide eaves.

A weatherboarded church was built at Pipers River in 1912 (Henslowe 1978) (pl. 12). For St Alban's, North returned to the idea of a ridge-mounted belfry and spire as at Parattah, but he rotated the hexagon so that two angles of it rested on the ridge, and the apparent belfry is without a bell and enclosed with small weatherboards; it is purely symbolic. The sharp metal-clad spire is hexangular, its timbers continuous with those of the dumb belfry. As at Parattah, the flared skirt of the spire makes a clear separation between it and the belfry.

For his home parish of Exeter, North designed in 1916 a plain but elegantly proportioned and detailed church to be built of local brick, with a square tower topped again with a louvred belfry and broad spire (Henslowe 1978) (pl. 13). As at Lachlan, the tower of All Saints contains the vestry, so it is placed near the holy end, and here that is towards the street, for this church is approximately oriented, altar towards the east, so the entrance is at the end distant from the street. The hand-moulded bricks

Plate 10 — Christ Church, Illawarra (Tasmania), Alexander North's transept and tower, the original schoolroom at left.

Plate 11 — Our Lady of the Sacred Heart, Mangana, a concrete church for a gold-mining town, decorated with inset glazed tiles.

Plate 12 — St Alban, Pipers River, a characteristic wooden country church by Alexander North; in this case the spire surmounts a false belfry.

Plate 13 — All Saints, Exeter, Alexander North's own parish church.

are of an unusual colour, made at James Edwards's Loira brickworks, the remnant of a dynasty that supplied bricks for Beaconsfield in the boom years (Nyman 1988). The building stands as a monument to North's paper on *The truthful treatment of brickwork* (North 1892), here executed by local builders. Alexander North lived, and died in this parish, so we can be sure he exercised his most careful supervision on the building of this little church, making it both economical and elegant.

The Methodists also built a church at Exeter in 1916 (Stanshall *et al.* 1976). It is a wooden building, but much less routine than many that had been built in the three decades before the Great War, for it is clearly the work of Alexander North, and if its generous and economically decorative windows did not make this clear, it is topped with the smallest of his ridge-mounted spires and belfries, this time square in plan and clad with sheet metal impressed with a fish-scale pattern.

It would appear that North had designed a church for the Methodists before, as early as 1891 (Stanshall 1976) (pl. 14). It was paid for by the local mining magnate, William Hart, and gifted to the church; and it still stands at Bryan Street, Invermay, confronting the viewer from Albion Street with the weirdest spire of all, square in plan and mounted diagonally on a small false belfry with squashed elliptical openings. The church has become a Tibetan Buddhist centre, and the spire must appear oddly familiar to those accustomed to some roof-forms of Central Asia.

The last, lowest, widest and cheapest of North's spires topped the Church of the Holy Family at Inveresk, built in 1930. It was a weatherboarded mission church of faintly cruciform shape with a tower clad with fibro-cement sheeting with cover strips painted to give a half-timbered effect. Despite its materials, its distinctive profile provided an impressive landmark in a flat industrial suburb. It did not overwhelm its humble neighbourhood, but greatly enhanced it until it was burnt down in 1971; its replacement provides little to inspire the viewer.

In his paper on *Rural Churches* (North 1905 n.p.), North argued strongly that small churches should not attempt to imitate great ones, that they should be true to their material, and when this was timber, it should not be in "imitation of pointed stone construction". "[A] pointed arch carried out in timber is a miserable sham", he roared, a manifestation of "that abominable debasement of construction known as 'carpenters' Gothic'". It would seem that North's metal-clad steeples were another expression of that philosophy. The visible supporting timbers or the louvred belfry below the splay clearly show that the intention is not to imitate masonry or brickwork; the steeples are made of what they are made of. Honest, practical, economical, but what of their form?

Plate 14 — Former Invermay Methodist Church, North's most sinister spire.

WHY SINISTER?

The fashionably "Gothic" perception of Alexander North's steeples raises a number of questions, some of them of historical interest. Is the perception entirely a projection of the viewer, conditioned by association of familiar images of story-book witches, or is it somehow inherent in the design? If it is inherent, was the effect in any way intended by North, or is it an incidental result of his chosen proportions? And if this last, why the repeated use of such proportions? Was the exaggerated horizontality and the varied verticality merely North's response to the hilly terrain of Tasmania?

The sinister appearance of Alexander North's steeples to many who view them today is largely attributable to association; many liken them to witches' hats. Several generations of children have been accustomed to witches in story-books wearing hats with a brim and a crown that comes to a sharp peak like a steeple, but that convention appears to date from the end of the nineteenth century and was probably not clearly established in the minds of former children at the time when the steeples were designed. The association appears to be peculiar to Western Europe and North America, and is an essential of the fancy dress of Hallowe'en as currently celebrated in the United States and its imitators. From the vantage point of adult life, the witches and their hats appear innocuous and even comic, but our response to the silhouette of a North steeple owes more to the frisson of fear that accompanied our earliest encounters with them.

Various explanations for the hat have been offered. One asserts that "steeple-crowned" hats were put on the heads of witches before they were burnt at the stake, possibly so that the holy symbol would attract the forgiveness of Heaven. Others associate it with the persecution of Quakers in America, or with the mediæval persecution of Jews in Europe, and link it with the traditional form of the dunce's cap, which has no brim (Jensen n.d.). The high point also evokes images of masked penitents in Spanish religious processions, and of the Klu Klux Klan.

In illustrated books for children published in the early nineteenth century, the characteristic hat is associated with old women wearing outdated costume, with no clear implication that they are witches (pl. 15). The holdings of the Osborne Collection of Early Children's Books at the Toronto Public Library include many with woodcut illustrations, including *The Talking Bird; or, Dame Trudge and Her Parrot,* printed in London in 1806 and *Mother Hubbard and Her Dog,* a chapbook published in Derby in about 1830 (De Vries 1965). Dame Trudge is shown wearing a black hat with a broad brim and a pointed crown, but the antics of her animals are attributed to the agency of the parrot, and not to any witchcraft on her part. The same is true of Mother Hubbard and her dog, but clearly the association between old women and performing animals stands in place of the idea of witches and their familiars.

The more direct association of the pointed hat with the female witch came in the early decades of the twentieth century with such illustrators as Arthur Rackham who gave them to some exceedingly repellent old women, but also to at least one pretty young witch riding a broomstick, and to Cinderella's fairy godmother. He also attributed them to a male wizard in his *Sleeping Beauty,* but that was as late as 1920. Rackham's work was equally popular and influential on both sides of the Atlantic, and although he was pre-eminent in the field, he was not alone.

The simultaneous appearance of North's sinister steeples and the children's book illustrations that have formed the mental association with them make it unlikely that such a connection was present in the mind of Alexander North. His devout Anglicanism with a probable tendency towards the Anglo-Catholic was far removed from any intention of satire or sacrilege. Our response to his work is a powerful demonstration of the validity of an associationist basis for aesthetic appreciation. The question remains: what was in North's mind when he drew those striking profiles?

North was clearly aware of the work of Viollet-le-Duc, and this awareness clearly went beyond a knowledge of the French master's mediæval reconstructions. The oddity of his more original designs clearly links him to other contemporary influences, notably to what has come to be known, principally in literature and painting, as Decadence. It was the time of Huysmans, Paul Verlaine, Aubrey Beardsley and Oscar Wilde. I am not aware of any authoritative attempts to identify a Decadent architecture, so I offer the topic to anyone in search of a subject for a PhD.

Think about the possible links between the graphic work of Aubrey Beardsley, which might bring a blush to the cheek of a Victorian young person, and that of Arthur Rackham, for whose illustrations she, a generation later, would have been the principal consumer. Stephen Romer, an English academic in a French University, has recently reminded us of the complexity of the *fin de siècle* in which Alexander North formed his ideas:

> *It was a period which saw, in no particular order, Bell's telephone, Edison's incandescent light-bulb, Pasteur's vaccines, the Eiffel Tower, [...] the first great department stores, free secular primary education for all, the legalization of divorce, the French can-can, child labour laws, anarchy, and the Dreyfus affair.* (Romer 2013 p. xiv)

Romer is looking at the era from a Continental perspective, but the flow of influences back and forth across the Channel was never interrupted, even by seventy years of conflict with revolutionary France, and North was working in the era of the *Entente Cordiale.* French *decadence* was alive and well in England, although mitigated in public at least by the Lord Chamberlain's regulations, the imprisonment of Oscar Wilde, academic conventions in the visual arts, literary censorship, and laws that made it necessary to import contraceptive devices as French letters. It was only a few years since the Ripper murders had torn the veil from the benign self-image of Victorian society. The darker underside of the Edwardian summer epitomised by Edwin Lutyens's mansions set in gardens by Gertrude Jekyll was more publicly evident than before. Did it find expression in architecture of the time, and particularly in church architecture, built to prevail against the "Gates of Hell"?

North would have been fully aware that mediæval churches were frequently provided, particularly on the outside, with carved images of pagan origin, some of them judged impious and obscene by later generations, "under the general rule that the gods of an older religion become the devils of a new faith" (Anderson 1988, p. 105). Those carvings that are more explicit than merely decorative have been variously understood as intended to ward off evil, or to show that it remains external, unable to penetrate the sanctuary within; they may represent persisting adherence to an older cult, or like some of the indoor carvings on misericords, a subversive wish to deride the clergy. Some may result from the mere fancy of the stone-carver, employed to embellish a fane, and paid by the day.

For the whole of the colonial nineteenth century, the few carved devices that appeared on churches in Tasmania were conventionally pious or neutrally vegetable. Other than the Catholic bishops' mitred monographs on some of Henry Hunter's churches, the only arguable exceptions are the heads that form the drips of the hood moulding above the door of St Luke's Church at Bothwell, carved by Daniel Herbert in about 1830, which Norman Laird held to be Celtic deities on the doubtful evidence of their head-dress; the male has a fine set of the mutton-chop whiskers that were becoming fashionable at the time, perhaps caricaturing a member of the colonial establishment (Laird 1971).

In his first major essay in Arts and Crafts Gothic Revival, Alexander North gave the exterior of Holy Trinity some more explicit intimations of evil, but they carry a hidden message of salvation. The drips of the moulding over the rose window of the north transept are contorted and

Plate 15 — Dame Trudge and her Parrot, J. Harris at the Original Juvenile Library, London 1808

foliated animals with huge haunches, reptilian tails and dog-like heads; antipodean monsters that owe something to the kangaroo as well as to the salamanders of European imagination. They are curiously ambiguous creations, for salamanders with their mythical ability to resist and quench fire were adopted in the middle ages as symbols of invincible faith, but here they are snarling like demons. In a similar situation on the south side, beside a window lighting the organ loft, the monsters are no longer foliated but winged, and so are their larger fellows on the kneelers of the east gable. They are not dragons but devils, for their wings are feathered and not webbed; in some biblical mythology, devils are held to be rebellious angels. These, fiercely snarling as they appear to be about to plunge, have had their wings clipped. These demons are not merely fallen angels; they are not swooping to encompass the damnation of the parishioners, but falling because they have been defeated, their powers curtailed.

These carvings, like the foliated decorations elsewhere on the church, were designed in detail by North, and realised by Hugh Cunningham (1858–1945). From the carvings, we can infer that North did not have a mediæval sense of the diabolical, but a more suitably moderate Anglican one. But he was a Churchman devout enough to build a chapel in his own house, so he probably had a personal sense of a cosmic conflict between good and evil. Yet his salamanders writhe because they are entangled with Art Nouveau Gothic foliage and not because they are enduring the fires of Hell; his devils are malevolent, but they will not prevail.

On a weatherboarded country church, such apotropaic devices were not affordable, but a splay-foot spire clad in sheet metal could perhaps provide shelter from more than rain, and at a time when Anglican certainties were under question as never before.

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(accepted 7 November 2017)

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